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# CONTENTS

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USAGE OF ANADROMOUS, CATADROMOUS AND ALLIED TERMS FOR MIGRATORY FISHES. By <i>George S. Myers</i> .....	89
TAGGING SALMON WITH BLOWGUN DARTS. By <i>Wm. Ellis Ripley</i> .....	97
THE SEMINAL VESICLES AND TESTES OF <i>Gillichthys</i> , A MARINE TELEOST. By <i>George F. Weisel</i> .....	101
BODY LENGTH OF THE SMALLMOUTH BASS AT SCALE FORMATION. By <i>W. Harry Everhart</i> .....	110
THE SYSTEMATIC STATUS OF <i>Plethopsis</i> WITH A DISCUSSION OF SPECIATION IN THE GENUS <i>Batrachoseps</i> . By <i>Robert C. Stebbins</i> and <i>Charles H. Lowe, Jr.</i> .....	116
BIPEDAL LOCOMOTION OF THE LIZARD <i>Basiliscus basiliscus</i> . By <i>Richard C. Snyder</i> ....	129
RECORDS OF <i>Macrochelys temminckii</i> IN OKLAHOMA. By <i>Bryan P. Glass</i> .....	138
A SEXUAL AGGREGATION OF THE GARTER SNAKE <i>Thamnophis butleri</i> (COPE). By <i>L. C. Finneran</i> .....	141
HERPETOLOGICAL NOTES—Notes on New-born Gaboon Vipers, by <i>Robert Snedigar</i> and <i>Emil J. Rokosky</i> : 145.—The Black-headed Snake in Southern Indiana, by <i>Sherman A. Minton, Jr.</i> : 146.—Notes on the Food of the Indigo Snake, by <i>William A. Babis</i> : 147.	
ICHTHYOLOGICAL NOTES—Field Notes on the Minnow, <i>Gila ditaenia</i> , in Southern Arizona, by <i>Loye Miller</i> : 148.—A Record of Lutjanid Fish ( <i>Lutjanus cyanopterus</i> ) for the Atlantic Coast of the United States, with Note on Related Species of the Genus, by <i>Luis Rene Rivas</i> : 150.—Goldeye, <i>Amphiodon alosoides</i> (Rafinesque), Occurring in Two Small Streams of Central Illinois, by <i>William C. Starrett</i> and <i>R. Weiden Larimore</i> : 152.—Embryological Notes on <i>Menidia</i> , by <i>Eugenie Clark</i> and <i>James M. Moulton</i> : 152.	
REVIEWS AND COMMENTS—The Life History of the Fish. His Morals and Manners: <i>Brian Curtis</i> , by <i>Gerald P. Cooper</i> : 154.—Fishes of the Western North Atlantic: <i>John Tee-Van</i> , <i>Henry B. Bigelow</i> , <i>Isabel Pérez Farfante</i> , and <i>William C. Schroeder</i> , by <i>Carl L. Hubbs</i> : 155.—Handbook of Frogs and Toads of the United States and Canada: <i>Albert Hazen Wright</i> and <i>Anna Allen Wright</i> , by <i>Helen T. Gaige</i> : 157.	
EDITORIAL NOTES AND NEWS—News Notes: 158.—Research on Poisonous Fishes: 158.	

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## Usage of Anadromous, Catadromous and Allied Terms for Migratory Fishes

By GEORGE S. MYERS

### INTRODUCTION

THE adjectives anadromous and catadromous are in common use by ichthyologists and biologists in general for fishes which migrate from salt to fresh water or from fresh to salt water to breed. However, this widely understood usage of these terms has been far from universal. Alexander Meek (1916), in the most important general work in English on fish migration, vastly broadened the scope of these terms by applying anadromous to any upward or shoreward migration, even in the sea, and catadromous to any seaward, offshore or downward migration. The authority of Meek's great work has caused a number of influential English-speaking biological writers, such as Kyle (1926: 53 *et seq.*) and J. Arthur Thomson (1929), to accept this wider usage. Even Scheuring, a German, in the most voluminous work yet published on fish migration, follows Meek (see especially Scheuring, 1929: 409). On the other hand, Regan (1929: see under "Breeding and Development") and Norman (1931: 265-266; 1937: 94-95), two of the most eminent of all ichthyologists, have preferred to ignore Meek's emendations. Furthermore, despite Meek, Kyle and Scheuring, most North American ichthyologists continue to use the adjectives anadromous and catadromous almost exclusively in the older, narrower sense, even though they may be quite aware of the broader usage of Meek.

### RUSSIAN USAGES

That there have been several rather important Russian papers on the terminology of migratory fishes seems to have escaped most non-Russian biologists. These papers are summarized in Peter Schmidt's book on migratory fishes (1936). Because this work appears to be almost unknown to the majority of biologists, cannot be read by most of them if it were, and is especially pertinent to our discussion, it seems useful to quote several passages from Schmidt. For the translation, the writer is indebted to Mr. Leo Shapovalov, of the California Division of Fish and Game.

Schmidt (1936: 17-19) says in part:

From the point of view of direction of migrations they may be divided, as proposed by Meek (1916), into anadromous and catadromous migrations . . . [Explanation of Meek's special usages of these terms and of *denatant* and *contranatant*.] This classification of Meek, however, is of small convenience, since later on we shall see that nearly every migratory fish is "anadromous" in one period of its life and "catadromous" [that is, in the sense of Meek] in another, and similarly may at different times be "denatant" and "contranatant."

A number of other authors have attempted to present not so much a system of migrations as a biological classification of fishes in general. Thus, Kessler (1877) distinguishes fishes, according to their life and environment, by the following groupings: (1) marine, effecting migrations only in the sea and approaching the shores from the depths; (2) brackish-water, living and shifting about in the brackish water of bays, lakes, and the estuaries of rivers; (3) diverse-water, able to live in fresh, brackish and

even salt-water; (4) through-running, living in seas or brackish lakes ascending rivers for propagation; (5) semi-through-running, spending part of their life in brackish waters, but also able to live in fresh waters and spawning only in fresh waters; and (6) fresh-water, dwelling only in the fresh water of rivers and lakes. Each of these groups is characterized by migrations within the indicated limits. . . .

Smirnov (1924), defining more precisely the scheme presented by Kessler, also lays down, as the basis of his own scheme, the principle of the relationship of the fish to salinity ["halinity"] of the water, and differentiates two periods in the life of the fish, the period of feeding or growth—the *trophic*—and the period of reproduction—the *generative*.

In degree of salinity of water he recognizes three gradations: fresh water (more precisely, slightly saline, since fresh water also contains salts), water of medium salinity, and water of high salinity, and the fishes preferring these gradations are called *oligo-*, *meso-*, and *polyhaline*. Fishes able to live in all three media are called *euryhaline* and those able to transfer from one gradation to the next, *through-haline*. For each fish there is created a formula expressing its relation in the trophic and in the generative period, so that, for example, the chum salmon, which lives in the sea and ascends rivers for spawning, will be a fish "generatively-oligohaline and trophically-polyhaline or individually euryhaline," which may be expressed by the formula "g. oh + t. ph = i. ch." Aside from the cumbersomeness and awkwardness of such determinations and formulas, they add little from the point of view of classification. . . .

Meissner (1933), having summarized all the preceding attempts . . . presents the most complete and detailed scheme, which, however, also suffers from cumbersomeness . . . As a result [of Meissner's work] the following emerges:

#### I. MARINE FISHES

- A. PELAGIC, living in the body of the water.
  - 1. *Schooling*, wandering in large schools.
  - 2. *Temporarily schooling*, gathering in schools periodically.
  - 3. *Living scattered*.
- B. BOTTOM FISHES
  - 1. *Schooling*.
  - 2. *Living scattered*.
    - a. Migratory.
    - b. Sedentary.

#### II. THROUGH-RUNNING FISHES

- A. TROPHICALLY MARINE, living in the sea.
  - 1. *Pelagic*.
    - a. Generatively brackish-water, propagating in certain parts of the sea.
    - b. Generatively fresh-water, propagating in fresh-water, running (rheophilic) or standing (stagnophilic).
  - 2. *Bottom*.
    - a. Generatively fresh-water stagnophilic.
    - b. Generatively fresh-water rheophilic.
- B. TROPHICALLY BRACKISH-WATER, but generatively marine.
- C. TROPHICALLY FRESH-WATER, but generatively marine.

#### III. SEMI-THROUGH-RUNNING FISHES

- a. Generatively rheophilic.
- b. Generatively stagnophilic.

#### IV. FRESH-WATER FISHES

- A. FISHES OF FLOWING WATERS (fluvial or rheophilic).
  - a. Generatively rheophilic.
  - b. Generatively stagnophilic.
- B. FISHES OF STANDING WATERS (lacustrine).
  - 1. *Pelagic*.
    - a. Generatively lacustrine.
    - b. Generatively fluvial.
  - 2. *Bottom*.
- C. FISHES OF FRESH-WATERS IN GENERAL; living indifferently in standing or running water and passing from one to the other.



This newest scheme is the most complete and embraces nearly all of the most important biological periods in the life of fishes. It should be expanded somewhat only in the field of marine fishes, since it is absolutely necessary to separate into specific groups the deep-water fishes, bottom and bathypelagic, and the semi-deep-water fishes, dwelling in the bathyal region.

For our special purposes, however—for an examination of the migrations of fishes and an all-sided investigation of this biological phenomenon—we shall hold to a simpler ecological scheme, namely to examine . . . the migrations of pelagic marine fishes, bottom marine fishes, through-running and semi-through-running fishes, and fresh-water fishes . . . We should not forget that our systems of classification are artificial. The life of organisms so mobile and readily adjustable to the environment as fishes is plastic, and fits with difficulty into schemes created by us.

#### HEAPE'S WORK ON MIGRATION

Most all of the general papers treating of migratory fishes were published before the appearance of Heape's great study of emigration, migration and nomadism in animals (1931), and Schmidt's work, although published in 1936, makes no mention of it. Heape's book is perhaps the most important single work on the movements of animal populations. Although few of his ideas were totally new, his critical study for the first time brought order into the migrational phases of ecology, and clearly distinguished the several distinctive types of population movements which most writers had previously uncritically lumped under "migration." It is notable that Heape not only directly and severely criticised Meek's broadening of the meanings of anadromous and catadromous (p. 264) but also clearly demonstrated, through his interpretations of Meek's accounts of the movements of various fishes, how confusing Meek's terminology really is.

Heape carefully and clearly separates *emigration* (a one-way moving out with no return) and *nomadism* (more or less aimless and homeless wandering) from *migration*. He distinguishes three general kinds of migration, the most important of which he calls "gametic migration" or breeding migration—a regular seasonal movement to breeding grounds at a distance from most or all of the normal range of the species. Besides gametic migration he also distinguishes "climatic migration" and "alimentary migration," both of them regular seasonal migrations which are "undertaken for the sake of self-preservation," because of either food or climatic factors. Heape dealt chiefly with terrestrial animals, and the writer does not find that he considered a possible fourth type which, for want of a better term, might be called "osmoregulatory migration," and which is to be seen chiefly in aquatic animals. This is a migration which is not a breeding migration but one based upon the necessity (for some as yet unknown physiological reason) of reaching and remaining in salt water for a period, in fresh-water fishes, or fresh water in salt-water fishes, during a particular period of the life-cycle. Such a migration occurs in the young of the fresh-water gobies *Sicydium* and *Sicyopterus* (Manacop, 1941) and is perhaps concerned in the regular fresh-water incursions of many marine fishes (for possible example, see Heape, p. 283, on *Megalops* and *Chanos*). Naturally, it is possible that such migrations are in whole or in part alimental migrations, but it seems very likely that some rhythmical physiological need of fresh or salt water may be even more compelling than food. Indeed, physiological reasons of

various sorts are probably involved in all these types of true migration, quite apart from the simple need for a certain food, climate, breeding site, or salt-concentration, and future work may demonstrate the impossibility of always sharply separating Heape's three types.

However, it should be remembered that Heape's exclusion of emigration and nomadism from true migration seems to be a perfectly valid and useful thing in fish study, with the understanding that next to nothing is yet known of mass emigration among fishes.

The two examples of mass fish emigration given by Heape (p. 129) are almost certainly not such. He has most curiously misinterpreted accounts of the development of exploration of the range of the tile-fish as emigration, whilst the halibut probably represents mere normal diffusion (with or without climatic change) and drift emigration, coupled with overfishing on the banks and consequent fishery exploration of the hitherto overlooked deeper parts of the habitat. On the other hand, nomadism is certainly of rather wide occurrence among fishes, although Heape's examples, drawn almost entirely from Meek, are not too convincing or well chosen. The pelagic and bathypelagic fish faunas, in particular, should present many examples of true nomadism, although this will be hard to prove for the smaller and deep-water forms.

#### NEED FOR REVISION OF FISH MIGRATIONAL TERMS

It should be evident that the usage of terms for migratory fishes is in considerable confusion and that some terminological revision is necessary, especially in view of Heape's work. Russian usage has varied from the complicated system of Meissner to that of Schmidt, who appears to eschew using even the conservative terms catadromous and anadromous. Some of the most important British and German writers on the subject accept these two terms but in a broad sense quite different from that commonly understood by American and Canadian ichthyologists and fishery biologists.

This varying usage of anadromous and catadromous has troubled the writer intermittently for a number of years, particularly in the teaching of ichthyology to university students. Moreover, in attempting recently to discuss migratory, euryhaline fishes in connection with some zoogeographical work, he has found the accepted terminology so poor and its usage so unstable that any attempt to be exact necessitates prolixity and any endeavor to be brief results in vagueness. Obviously some revision of the terminology is necessary.

#### PROPOSAL OF A REVISED TERMINOLOGY

In considering the terminology of fish migration one fact must be kept in view—that the meanings of words are determined by general usage. There can be no doubt, considering the literature of ichthyology in general and the common usage of North American ichthyologists and fishery biologists in particular, that general usage of the terms anadromous and catadromous is in the older, narrower sense and not in the wider one of Meek. It would therefore certainly be most unwise to try to disturb common usage of these terms.

So far as other general terms are concerned, the obvious thing to do is to

accept Heape's definitions of nomadism, emigration, migration, and subsidiary terms, even though most ichthyologists are scarcely aware of them, simply because ecologists in general have done so and wide ecological usage may be expected to spread among fish ecologists. But the only one of Heape's terms which especially concerns us here is migration, which the writer temporarily calls "true migration" to distinguish it from looser previous usages.

Having thus decided that Heape's usage of migration, and the current restricted usage of anadromous and catadromous must be accepted, we are still faced with some difficulties, simply because the only other terms in any general use among biologists writing in English are *denatant* and *contranatant* (see Meek: 19) and these are quite inadequate for the type of work we have in mind. It would seem, then, that several other terms would be useful, perhaps not for ordinary use but for special situations where existing terms do not give sufficient precision. The writer's strong aversion to the infliction of new scientific terms upon the scientific public has, however, caused him to proceed with great circumspection. Moreover, Schmidt's concluding statement (see above), that the ways of living organisms fit with difficulty into any man-made categorical classification, is particularly apt.

Nevertheless, acceptance of the narrower usage of anadromous and catadromous does necessitate the proposal of other terms, and the fact that the rich terminological crop that has sprouted in the Russian literature is almost wholly in the Russian language prohibits direct utilization of most of the terms in English. Terms of classical derivation, such as anadromous and catadromous, would be much better, simply because, with only minor changes, they are widely acceptable in many languages. Finally, the writer has ventured to propose new terms only because he feels that certain new terms will be of distinct advantage in some specialized types of ichthyological work, and that the general biologist and fishery worker will seldom or never have to bother his head about them. Catadromous and anadromous will almost certainly always remain the most important and probably the only widely used terms of their class. With this understanding, we may proceed to the terminological system proposed.

The most practical system of classifying fish migrations would seem to be one based principally upon the physical type of route and direction followed, and this method of classification is implicit in the already well accepted terms anadromous and catadromous. But the exact types of migrations exhibited among the 25,000 or more living species of fishes must be exceedingly varied, and as continuing study brings our knowledge nearer to completeness, we may confidently expect the known types to increase and apparent differences to be bridged over. For this reason the writer has attempted to keep the terminology proposed as simple and as general as possible. He proposes the following terms, some of them new.

*Diadromous*. Truly migratory fishes which migrate between the sea and fresh water. There has been no English term by which one can refer collectively and briefly to anadromous, catadromous and other fishes which truly migrate between fresh and salt water, and this new term is now proposed for such occasional use as it may have. Like the two well known

ones, this adjective is formed from classical Greek (*δια*, through; and *δρομος*, running). Little more need be said in its behalf. This term is almost or quite equivalent to the Russian term, "through-running," as used by Kessler (1877), Meissner (1933) and even Schmidt (1936), although it was coined before the writer was aware of the Russian literature.

*Anadromous*. Diadromous fishes which spend most of their lives in the sea and migrate to fresh water to breed (From *ἀνα*, up; and *δρομος*). Examples: *Roccus*, *Oncorhynchus*, *Salmo salar*, *Alosa*, sea-lampreys, etc. The term is used principally for fishes which run up rivers to spawn, but has upon occasion been applied to fresh-water lacustrine species which "anadromously" run up streams flowing into the lake habitat. The writer sees no incongruity in such a natural transposition, especially if it is made clear that the migration is a potamodromous one, but it would certainly be less confusing to say (as above) that such lake species "run up tributaries anadromously" than boldly to label them as "anadromous." There is also the question of labelling marine fishes which run up into estuaries, brackish water, or almost fresh water to spawn, but the common usage of anadromous would exclude them and the small use a special term would have militates against proposing one. Gunter (1942) has discussed borderline cases.

*Catadromous*. Diadromous fishes which spend most of their lives in fresh water and migrate to the sea to breed. (From *κάτα*, down; and *δρομος*.) Examples: *Anguilla*, some *Galaxias*, probably many gobies. There has never been much variation in the general usage of this term, although when the life-histories of many small gobies and other fishes become known there may be some question in regard to how far into brackish or salt water a fish must go to be called catadromous. The comment would be similar to that under anadromous. The mullet, *Agonostomus*, may perhaps be added to the small known list of truly catadromous fishes. Dr. C. L. Hubbs tells the writer that he has found the "Querimana" stage of this genus "in completely salt water in Acapulco Bay," Mexico, but it is, of course, possible that *Agonostomus* may belong in the next division.

*Amphidromous*. Diadromous fishes whose migration from fresh water to the sea, or vice-versa, is not for the purpose of breeding, but occurs regularly at some other definite stage of the life-cycle. (From *ἀμφι*, around, on both sides; and *δρομος*.) This new term is proposed for a small known (but undoubtedly really large) number of species which appear to need to visit salt, or conversely, fresh water, at some period of the life cycle other than the breeding period. The prototype is the goby genus *Sicydium* and its close allies, common in tropical fresh waters round the world. These fishes live and spawn in swift water, but the larvae float downstream to salt water where they remain for a time before migrating back upstream as small fry (Manacop, 1941). Upon the catching of these fry is dependent the *ipon* industry of the Philippines. Marine amphidromous fishes which migrate into fresh water are probably more numerous than suspected, especially among such families as the Mugilidae. *Megalops* and *Chanos* may also belong here. It should be noted that amphidromous migrations are not gametic migrations in the sense of Heape and the fact that they are not is one reason for recognizing them as a distinct type.

*Potamodromous*. Truly migratory fishes whose migrations occur wholly within fresh water. (From ποταμος, river; and δρομος.) Examples: *Salminus*, *Prochilodus*, *Moxostoma*, *Labeo*, etc. This term is proposed especially for those exceedingly numerous species of fluviatile fishes (particularly in the tropics) which migrate long distances upstream to spawn, but is also available if necessary for any truly migratory, permanently fresh-water fish. In practical work, the term would almost certainly be used chiefly for such spectacular migrants as *Salminus* and *Prochilodus*, since the vertical or shoreward breeding migrations of lacustrine fishes can and will undoubtedly be called simply that (but see also under oceanodromous). The same applies to such common but as yet almost unstudied breeding migrations as those of tropical fluviatile fishes from the stream into the flooded forest during high water. And few will care to label formally as migrations the slight movement from a river channel to a shallow sand-bar for spawning; it will usually be described simply as a "movement from .... to ....," no matter how true a migration it may be in the sense of Heape.

*Oceanodromous*. Truly migratory fishes which live and migrate wholly in the sea. (From Ὠκεανος, the ocean; and δρομος.) Examples: tunas, herrings and large numbers of other marine fishes. Of course, we might call these "marine migratory fishes," but most anadromous fishes would be classified as "marine migratory fishes," yet they migrate into fresh water. The new term has a definite specialized use. There are many wholly distinct types of migrations lumped here which it may be useful to name at some future date, but the writer does not like to go farther. The adjectives denatant, contranatant, seaward, shoreward, offshore, onshore, vertical, downward, upward, diurnal, nocturnal, etc., certainly provide enough terms to cover most of these migrational types quite well without the continued use of anadromous or catadromous for oceanodromous fishes (which is definitely contra-indicated by common usage, as already explained above). If marine or lake biologists *must* have technical terms for migrations to deeper and to shallower water, it would be less confusing to have distinctive ones such as *Bathydromous* (βαθvs, deep) for the former and *Bracheadromous* (βραχεα, shallows) for the latter, although the writer doubts that such terms would ever be much used.

Finally, there are certain fishes whose movements are not covered by any of the general terms here used, but the writer doubts that many of these movements can be described as true migrations in the sense of Heape. *Gasterosteus aculeatus* is commonly given as a typical euryhaline non-migratory fish, yet the unpublished observations of Mr. Leo Shapovalov on this species in Scott Creek, California, demonstrate clearly that seasonal denatant migrations or emigrations occur. It is difficult to characterize such a fish, if it really is migratory. Truly non-migratory, euryhaline species do occur, although good and undoubted examples are hard to find. The best ones known to the writer are the viviparous cyprinodonts *Mollienisia latipinna* and *Poecilia vivipara*; in Brazil the latter breeds in the Rio Parahyba over 100 miles from the sea, and likewise among mangrove roots at Florianopolis, in pure sea water (personal observation). *Fundulus heteroclitus* is as good an example. On the east coast it spawns in pure sea water yet

Hubbs and Lagler report its acclimatization in the Ohio basin in Pennsylvania. Apparently certain boreal marine fishes (such as *Myoxocephalus*; Ekman, 1935: 205) tend to enter fresh water more readily towards the colder parts of their ranges, and certain tropical ones (*Pristidae*, etc.) do so towards the warmest regions. On the other hand, *Gasterosteus aculeatus*, a member of a northern family, becomes more strictly fluviatile southward.

## ACKNOWLEDGEMENTS

The writer is indebted to Mr. Leo Shapovalov not only for the Russian translation given but also for notes on *Gasterosteus*. Dr. Carl L. Hubbs has offered several very helpful suggestions, including those of the terms *amphidromous* and "osmoregulatory migrations," although he is not to be held responsible for the proposal of these terms.

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NATURAL HISTORY MUSEUM, STANFORD, CALIFORNIA.

## Tagging Salmon with Blowgun Darts

By WM. ELLIS RIPLEY

IN 1944 the largest fall run of king salmon (*Oncorhynchus tshawytscha*) ever observed on the Tuolumne River was recorded at the Modesto count-

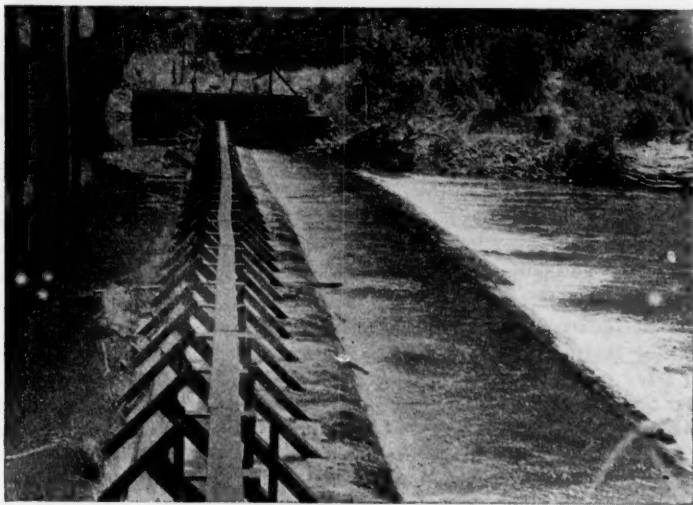


Fig. 1. View of Modesto dam looking south.

ing station. A low, removable dam, extending across the river, is maintained at this point by the city of Modesto, California. At the north end is installed a fish ladder which permits passage of the salmon around the barrier to the

spawning areas in the river above. This ladder is the only station on the river where observations can be made on the number of fish making the spawning migration.

During the peak day of the run more than 10,000 fish passed through the counting gate. Because of the large numbers of fish present, many salmon could be seen on the apron and in the shallows immediately below the dam. As these fish were visible from the U. S. 99 Highway Bridge that crosses the river over the dam, tourists, sportsmen, and other observers gathered in great numbers to watch the salmon. Some of the more vociferous members of this group contended that, because so many fish could be seen below the dam, the dam must be blocking the fish and thereby endangering the run. The channel of the river follows along the south bank, and many salmon make their first appearance at the south end of the weir and work their way across the apron to the fish ladder on the north side. The validity of the theory expounded by some of the observers, that the fish took as much as two or three days to find their way across the dam to the ladder and that the dam was blocking the run of fish, was difficult to determine without concrete evidence. That the large number of fish visible was merely the result of the presence of a large natural run of fish in the river was not considered possible by the onlookers, and much agitation was engendered to lower the dam and free the fish. Obviously this could not be done without curtailing the spawning population estimates and seriously limiting the investigational studies of this river.

To appraise these claims, it was necessary to devise a method of tagging that would give some index of the time required by a salmon to work along the apron and find its way through the fish ladder. The customary technique of catching, marking, and returning the fish to the water was not considered practical because the problem did not warrant the amount of effort involved; and also effects on the salmon of the attendant excitement and stimulus associated with this type of tagging might introduce reactions that would make the results inaccurate. As the duration of the tagging experiment was quite limited, it was decided to use a modified dart tag that could be placed at the base of the dorsal fin while the fish was in the water. It was found that when the dart was inserted at an angle of 15 to 60 degrees from the vertical, the basal rays offered excellent purchase for the barbed point.

The tagging darts consisted of straightened No. 5/0 fish hooks cut off 1-1/2 inches from the point. A regular celluloid tagging disk was placed over the shank, and a drop of solder was attached to the end to prevent the disk from coming off when the shaft was driven into the salmon. A No. 5 cork cut to fit snugly within the bore of a one-half inch, thin-wall, electrical conduit tube was placed over the soldered end of the dart shaft. When properly projected, the barbed shaft was driven its entire length into the base of the dorsal fin with the tag disk snug against the skin, and the cork was forced off the end of the shaft, exposing the disk. The tagging dart was placed in the breach of the tube with the point facing the muzzle, and the dart ejected by a sudden puff of air. This latter operation can best be compared to a cough. A normal amount of air is taken into the lungs and then expelled through the tube by a sudden contraction of the diaphragm.



It should be noted here that the speed and accuracy with which the dart travels is the result of the sharpness of the expulsion rather than the quantity of the puff.

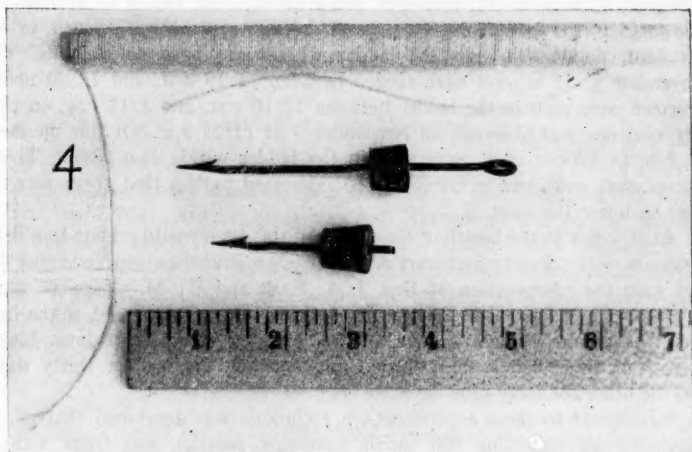
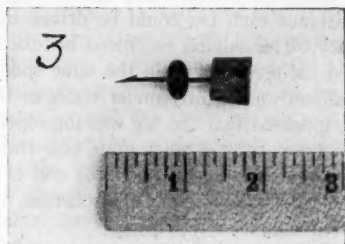
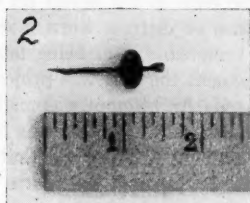


Fig. 2. Tagging dart showing lead stop.

Fig. 3. Tagging dart with cork attached.

Fig. 4. Blow gun harpoon equipment. The upper object is the tapered dowel with the retrieving line coiled about it.

A tube about 3 feet in length is satisfactory. This is aimed laterally with both eyes focused on the target, and with the point of aim midway between the end of the two apparent tubes that appear because of parallax. Vertical compensation for distance is best learned by experience. However, a sight, the length of which is the same as that of the distance between the eye and the mouth, can be mounted perpendicularly on the muzzle end of the tube to facilitate elevation. Sufficient accuracy can be developed quickly

with this device. A beginner can soon learn to hit consistently an area the size of a cigarette package at a distance of 15 feet.

The salmon were tagged at the south end of the dam within 10 feet of shore where there were many fish finning with their backs out of water. At this distance each tag could be driven into the base of the dorsal fin with accuracy. The salmon exhibited no discomfiture or distress when marked, most of them remaining in the same spot for some time after being tagged. One salmon was slightly under water at the moment the dart was projected, and it appeared that the tag was improperly fixed. An attempt was made to remove the dart by a quick grab, but when the fish (a 3 pounder) was lifted out of water, suspended upon the end of the barb, it was decided that the tag was adequately fixed. This action, unlike the tagging, did alarm this particular fish.

On November 6, 19 salmon were tagged by this method between 8:35 and 8:45 A.M. at the south corner of the dam. Due to the turbid condition of the water and the speed with which the fish were passing through the ladder, it is probable that several of the tagged fish escaped observation. However, 12 tagged fish were seen going through the ladder as a result of this tagging, the first at 9:05 A.M., and the last at 2:32 P.M., 5 fish, or 42 per cent, passing through the ladder within two hours of tagging. On November 8, 35 salmon were tagged between 11:15 A.M. and 12:00 noon. Thirteen were seen in the ladder between 12:10 P.M. and 3:11 P.M. on this day, and one was observed on November 9 at 12:25 P.M. Of this number, 10 fish, or 80 per cent, were seen in the ladder within two hours. These figures were sufficient to convince the interested parties that there was no need to lower the dam.

As an index to the length of time a tag of this type would remain in a fish, 6 salmon were taken to Steinhart Aquarium, San Francisco, on November 15 and with the co-operation of Drs. J. A. Kask and W. M. Chapman were tagged and held in tanks. The results indicated that 50 per cent of the fish shed their marks within two days, and 100 per cent within eight days. However, 2 of these fish were re-tagged and one held its tag for thirty days and the other for forty-nine days.

Subsequent to these experiments, a technique was developed that offers possibility for collecting fish, small mammals, reptiles, and frogs with a harpoon dart. A barbed dart made out of a straightened No. 9/0 fish hook, either with or without the eye, fastened to a coil of No. 6 medium-laid seine twine, was found to make a very satisfactory harpoon. To facilitate insertion of the line into the blow gun tube, the line is coiled on a slightly tapered dowel about 9 inches long. The dart is tied to the line, inserted into the tube, and followed by the dowel with the coiled line. The dowel is removed by holding the last few coils of line and twisting the dowel in the opposite direction to the coils, leaving the line coiled in the tube ready for firing. Maximum accurate range with this modification is about 30 feet. It is a most successful device for capturing frogs.

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## The Seminal Vesicles and Testes of *Gillichthys*, a Marine Teleost<sup>1</sup>

By GEORGE F. WEISEL

GLANDULAR structures accessory to the testes of some fish have received scant attention. So-called seminal vesicles were noted as early as 1824 by Rathke in *Gobius niger*. The double seminal vesicles of *Mullus barbatus*, *Gobius jazzo*, *G. minutus*, *G. panganelus* and the single vesicle of *Cobitis fossilis* were briefly described by Hyrtl (1850). An excellent study of the sexual organs of several species of gobies and blennies was made by Eggert (1931). He reported in detail the structure and histology of the seminal vesicle of *Periophthalmus chrysopilus*. In *Esox lucius*, Disselhorst (1904) recognized similar structures, but only in large males during spawning time. Gilbert (1943) gave an account of the seminal vesicles of *Chlamydoselachus*.

The male mudsucker, *Gillichthys mirabilis*, has well developed accessory sex organs. Although this fish is common in the bays and estuaries along the Pacific coast of the United States, the testes and vesicles have not been previously described. This report also includes observations on the seasonal changes in the testes and vesicles, the possible function of the vesicular fluid, and the response of the vesicles to testosterone.

### MATERIALS AND METHODS

To determine the seasonal changes in their reproductive tracts, mature male mudsuckers were collected near San Diego, California, in February, March, April, May, August, September and November. The genital papillae were measured across their greatest length and width with a micrometer in the ocular of a dissecting microscope. The testes and seminal vesicles were fixed in Bouin's and after sectioning were stained with hematoxylin and eosin. Some of the sections were also stained with iron hematoxylin or Mallory's triple connective-tissue stain.

### STRUCTURE OF THE SEXUAL ORGANS

The male sexual organs of *Gillichthys* consist of the paired thread-like testes, the spermatic ducts, the seminal vesicles and the urogenital papilla.

For the size of the fish (the adults average about 12 cm. in length), the testes are very small. Even during the spawning season they rarely exceed 2 mm. in diameter. The cysts of maturing germ-cells and the spermatozoa are contained in thin-walled lobules. The lobules are usually fused near their bases, where they open into the spermatic duct (Fig. 1), but the distal ends are free. Two to six lobules may lie laterally in the longitudinal series.

In comparison with many teleosts, *Gillichthys* has a simple type of testis. The lobules are simple sacs with few or no trabeculae, instead of the complex network as found in the perch (Turner, 1919), *Cottus* (Hann, 1927), the

<sup>1</sup> Contributions from the Scripps Institution of Oceanography, New Series, No. 423. I wish to express my gratitude to Dr. Carl L. Hubbs and Dr. Boris Krichesky of the University of California for suggesting changes in this paper.

poeciliids (Geiser, 1921; Vaupel, 1929; Matthews, 1938) and the Pacific salmon (Weisel, 1943). The lobules project individually from the spermatic duct, rather than being bound tightly together by the connective tissue sheath. The walls of the lobules are covered with peritoneal epithelium, which continues dorsally and secures the testis and spermatic duct anteriorly to the air bladder and posteriorly to the kidneys. The lobule walls consist principally of connective tissue fibers. Through this tissue course the capillaries which evidently arise from the main testicular vessels that run parallel with and in the wall of the spermatic duct. No interstitial tissue was found, such as Eggert (1931) described for a related species, *Gobius auratus*.

The lobules empty directly into the spermatic duct which lies dorsal to them. The duct is generally single. It is lined with cuboidal or squamous epithelium. The surrounding layer of connective tissue and smooth muscle is thicker than that of the lobular walls. At its posterior extremity the duct from each testis enters a common pore in the genital papilla.

The spermatic duct has ventrally projecting lobules for its entire length until it reaches a position ventral to the urinary bladder. At this point there arises the comparatively large fanshaped seminal vesicle (Fig. 2). This organ has the appearance of greatly enlarged lobules which contain a bright yellow fluid rather than the milky substance of the testes. The anterior lobes of the vesicle seem to be a graduation from the testicular to the vesicular lobules. Serial sections prove that there is such a transition. The epithelium lining the lobules in this transitional zone is partially secretory and partially germinal. Beneath the peritoneum, which covers the external surface of the vesicle, lies a thin layer of connective tissue and smooth muscle. The connective tissue layer is heaviest at the basal portion, where the ducts of the seminal vesicle are in direct communication with the spermatic duct. The larger blood vessels are in this region. The layer of connective tissue becomes progressively thinner toward the distal end of the vesicle and contains only small blood vessels.

The internal surface of the vesicle is covered with a continuous epithelium. The epithelial cells are undoubtedly secretory. Their appearance conforms with the excellent description given by Eggert (1931) for the seminal vesicles of *Periophthalmus chrysospilos*. Eggert distinguished two types of secretory cells in the vesicles of *Periophthalmus*. My observations revealed only one type in *Gillichthys*, and the vesicular fluid contains no discrete droplets. The species of *Gobius* investigated by Eggert likewise produce only one type of secretion.

When the cavities of the vesicles are distended with fluid the epithelial cells are squamous. In vesicles which contain little or no fluid the epithelium is mostly cuboidal to columnar. The cells lining the base of the vesicular lumen are more columnar than are those in the distal end. The nuclei are generally basal and only infrequently centrally located. Eggert believes that secretion occurs principally in the distal and central portion of the vesicle. My observations agree with those of Eggert.

With the exception of a few spermatozoa found at the base of the seminal vesicle, where it joins with the spermatic duct, and in the transitional lobules, spermatozoa are not found in the vesicle. At these locations the spermatozoa

and the vesicular fluid are mixed, but the organ undoubtedly never serves for the storage of spermatozoa.

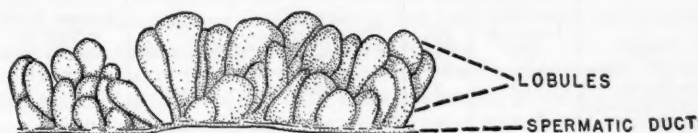


Fig. 1. Detail of a portion of testis of *Gillichthys*.

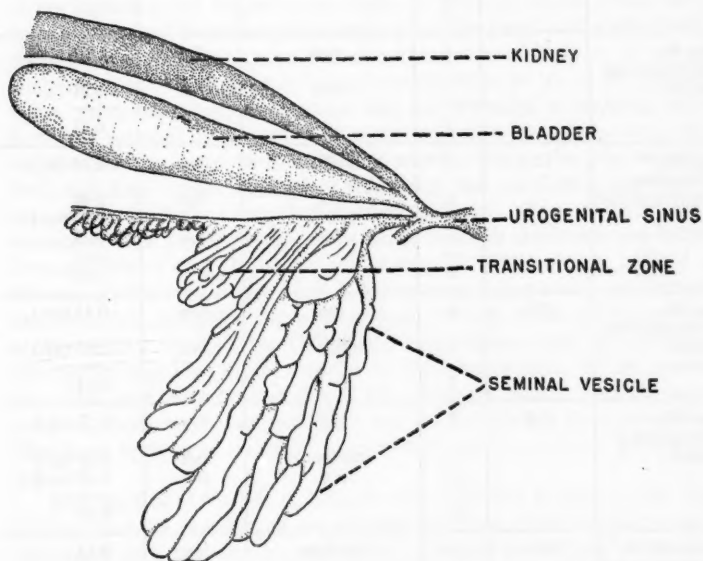


Fig. 2. Detail of the "seminal vesicle" and related urogenital system of *Gillichthys*.

#### SEASONAL CHANGES

The seasonal changes in the vesicle were determined and were correlated with the condition of the testes. Particular effort was made to obtain males of the same size at different months for such a study. Examination of ovaries and young had already shown that *Gillichthys* has a long breeding period, ex-

TABLE I  
SEASONAL CHANGES IN THE TESTES AND THE "SEMINAL VESICLES"

Date	Average Standard Length in cms.	Condition of Testes			Average Widths of Vesicular Lumen in mms.†
		No. Fish	Cysts of Spermatogonia & Spermatocytes*	Spermatozoa	
Feb. 28, '46 Early spawning period	11.4	1	medium	few	0.27
		1	few	full	0.35
		3	none	full	0.25 (av.)
		5			0.29
April 5, Mid-spawning period	11.8	1	few	full	0.36
		1	few	few	0.10
		2			0.23
May 18, Mid-spawning period	12.2	4	none	full	0.32 (av.)
		1	none	few	0.21
		5			0.27
Aug. 15, Early post-spawning period	12.3	2	medium	few	0.36 (av.)
		1	few	full	0.40
		2	none	full	0.23 (av.)
		1	none	few	0.29
		6			0.32
Sept. 12, Post-spawning period	12.6	4	full	few	0.44 (av.)
		3	medium	few	0.43 (av.)
		7			0.44
Nov. 29, Pre-spawning period	11.6	2	full	few	0.27 (av.)
		6	medium	full	0.29 (av.)
		2	few	full	0.28 (av.)
		10			0.28
March 30, '47 Spawning period of next year	12.3	1	medium	few	0.33
		5	none	full	0.20 (av.)
		3	none	few	0.16 (av.)
		9			0.23

\* The number of spermatozoa and cysts of maturing germ-cells was set by qualitative impressions.

† The diameters of the lumen of ten sections from the central portion of the vesicles were measured for each fish.

tending from January to July (Weisel, 1947). Table I summarizes the germ-cell development in the testes and the average widths of the vesicular lumen during the pre- and post-spawning periods as well as for the spawning period.

The testes exhibited a definite seasonal cycle, but there were no sharp changes. Some spermatozoa were present in the testes the year around and spermatogenesis was continuous. At the height of the spawning period (March, April and May) the testes and spermatic ducts were packed with spermatozoa and had very few or no cysts of spermatocytes and spermatids. It was assumed that the act of spawning had just been completed in several individuals taken during these months as their testes had only a few spermatozoa in the lumen of their ducts and lobules. The spermatozoa were few but the lobules were filled with cysts of maturing germ-cells in the post-spawning period in September. Some of the testes from fish taken in August showed this condition whereas others were like those in the spawning months. By the last of November, which is in the pre-spawning period, the spermatozoa again increased greatly in number and the cysts of germ-cells decreased proportionately.

Seasonal changes in the seminal vesicles were less evident. Measurements of the epithelial cell heights as an index to secretory activity met with no success. The cell heights varied greatly from the basal to the distal end of the vesicle and even in sections the same distance from the base. A statistical analysis of the measurements taken proved them to be of no significant value. Also, the position of nuclei and the intensity of staining did not show any seasonal differences. The gross and microscopic appearance of the vesicles was the same in the different months except that the amount of fluid was considerably reduced in fish which had, as determined from the examination of their testes, just finished spawning. As a criterion for the amount of fluid in the vesicles, the average width of the lumen was found to be more reliable than the weight of the vesicles. The averages indicate that the vesicles were most distended in the post-spawning month of September and that they contained the least amount of fluid in the spawning months of March and April (Table I), but this circumstance may be attributed to the partial emptying of the vesicles in the latter months by the spawning act. The most distended vesicles of fish which, as judged from the appearance of their testes, had evidently not yet completed their spawning in March or April were no larger than vesicles from post- and pre-spawning fish.

The papillae of the fish in different seasons varied greatly in size, but no indications were obtained of enlargement or other difference that could be correlated with the sexual cycle. The measurements, however, were made on preserved material, which undoubtedly did not fully or reliably represent the conditions in life. I have noticed that the papilla becomes suffused with blood and swollen in gravid females, but this was not observed in the males. Eggert (1931) stated that the papilla of the species of gobies he studied had an erectile tissue.

#### RESPONSE TO TESTOSTERONE

One of the most notable effects of androgens is on the Wolffian duct and its derivatives (Moore, 1939; Burrows, 1945). The response of the seminal vesicles of *Gillichthys* to testosterone was negative. This lends support to the morphological evidence that the vesicles do not arise from the Wolffian



duct and hence are not homologous with mammalian seminal vesicles. Mature male fish were injected intraperitoneally three times at 7-day intervals with 0.8 mg. methyl testosterone (Metandren, Ciba) or were treated by simply adding 5 mg. of powdered methyl testosterone or 8 mg. nonesterified testosterone per 20 liters of their standing aquaria water which was renewed every other day. The fish were killed for examination after 10 to 20 days of treatment. The seminal vesicles from treated fish were similar in weight and in histology to vesicles from control fish.

There is little doubt that androgens induce the nuptial coloration and mating behavior in certain fish (Noble and Borne, 1940; Burger, 1942). Daily observations were made to determine whether the male sex hormones would induce out of season the remarkable fighting behavior and color changes which *Gillichthys* show during their spawning period (Weisel, 1947). Neither fighting nor color changes were noticed. However, *Gillichthys* is a poor subject on which to detect the enhancement of breeding behavior by male hormones. Even during the spawning season, mating behavior occurs only when the mudsuckers are thoroughly accustomed to their tanks and have selected their territories and mates. Also, the black hue affected by *Gillichthys* during their mating is probably due to a nervous control of the chromatophores, as it appears and disappears in a few seconds. It is apparently not the same as the breeding coloration of many other fish, which is assumed gradually and is more or less permanent during the spawning season.

To check potency, the methyl testosterone and nonesterified testosterone samples were successfully tested on *Gambusia* females which had their anal fins clipped. Gonopodia were formed by all. The hormones were added to the water in the same dilutions as they were with *Gillichthys*. This does not deny the possibility that administration of larger quantities of the androgens would not have had noticeable effects on *Gillichthys*.

#### OBSERVATIONS ON THE FUNCTION OF THE VESICULAR FLUID

The function of the vesicular fluid is not known. Reports that it prolongs the life of the spermatozoa after spawning are not confirmed for *Gillichthys*. Eggert (1931) found that spermatozoa teased from the testes of *Gobius panizzae* maintain a lively activity for 30-35 minutes in sea water, but that, if he added vesicular fluid to the sea water, the spermatozoa maintain their activity for at least 50-60 minutes. Eggert concluded that "... geht deutlich hervor, dass das Samenblasensekret die Aufgabe besitzt, den Spermatozoen eine längere Bewegungsfähigkeit zu verleihen." Similar experiments were made with spermatozoa of *Gillichthys* by Young and Fox (1937) and by myself (Weisel, 1948). We agree that spermatozoa live as long in sea water as in sea water with vesicular fluid added.

Schlenk and Kahmann (1938) reported that spermatozoa from trout remain immobile until the sperm fluid is diluted, and that it is the potassium in this fluid which prevents movements of the spermatozoa in the undiluted fluid. This does not appear to be the case for the spermatozoa of *Gillichthys*. Spermatozoa from teased testes when placed in hanging-drop preparations of straight vesicular fluid remained inactive. When these same preparations



were diluted with sea water or fluid from the coelomic cavity of the fish, the spermatozoa became active immediately. Spermatozoa which had remained inactive in a drop of vesicular fluid for six hours were activated by addition of sea water, and the majority maintained this motility for two hours. Solutions of NaCl, KCl, MgCl<sub>2</sub>, and CaCl<sub>2</sub> with an osmotic pressure similar to sea water activated the spermatozoa lying dormant in the drop of vesicular fluid. These solutions also activated spermatozoa from teased testicular tissue with no vesicular fluid present. Dilutions of vesicular fluid with dextrose solutions which had an osmotic pressure the same as that of sea water also activated the spermatozoa. However, if the vesicular fluid was diluted with fresh water, the spermatozoa were not activated. Consequently, the activating factor of the sea water is not caused by a dilution of any of the vesicular constituents, nor by addition of specific ions in the sea water. Also motility is not induced by reducing the viscosity of the vesicular fluid when fresh water is added. The spermatozoa are not activated by a change in pH since they become motile in solutions ranging in pH from 4.8 to 10.1 (Weisel, 1948). The pH of the vesicular fluid is close to 7.2 (Young and Fox, 1937). It is more likely that activation is caused by change in osmotic pressure (Ellis and Jones, 1939).

It is possible that the vesicular fluid serves to keep the spermatozoa in an inactive state and to nourish them. This would apply only to the comparatively few spermatozoa in the basal chambers of the seminal vesicles as none of the typically staining vesicular fluid was found in the testes proper. Probably the true function of this fluid can only be determined by actual fertilization tests.

#### DISCUSSION

The seminal vesicles of the gobies are not a part of the Wolffian duct system and are in no way homologous with the accessory male organs of reptiles and mammals (Eggert, 1931). It is evident from morphological examination of the seminal vesicles of *Gillichthys* that they are similar to testicular lobules, but are specialized for secretion. This is clearly indicated in the transitional zone between the testis and the vesicle, where lobules have a mixed germinal and secretory epithelium.

The experiments with testosterone show that the seminal vesicle of the goby is unlike the true seminal vesicle (of mammals) physiologically as well as in embryonic origin. Since it is not a part of the Wolffian duct system, it is not surprising that male hormones do not favor its development.

Accessory sexual organs are more highly developed in the gobies and blennies than in many other types of bony fish. It is possible, however, that the spermatic ducts of many teleosts are secretory and perform the same function as these specialized outgrowths. Fish that possess no vesicle often have spermatic ducts which are tortuous and which are covered with what is apparently a secretory epithelium (Langer, 1913; Lickteig, 1913; Weisshaupt, 1925). I have re-examined the spermatic ducts from Pacific salmon, which were used in another study, and find that the epithelium lining the complicated ducts is similar to that of the seminal vesicles of *Gillichthys*.

The presence of an accessory sexual organ in *Gillichthys* may be related

to the small size of the testes. The weight of the vesicles far exceeds that of the testes themselves (four fish taken in August with an average body weight of 28.5 gm. had testes which averaged 13.2 mg., whereas the average weight of their vesicles was 32.5 mg.). Possibly the quantity of the spermatozoa can be reduced and fertilization still remain effective due to some action of the vesicular fluid. However, *Gillichthys* spawns in holes in mud-banks where the spermatozoa are less subjected to scattering by currents than are the spermatozoa of most other fish. Hence, the spermatozoa may not be required in such large quantities.

In correlation with the uniform climate in its range, the spawning season of *Gillichthys* is protracted and seasonal changes in the sexual organs are slight. Eggert (1931) concluded from his morphological investigations that the seminal vesicles are secretory and that in the northern species of blennies the secretory activity parallels the ripening of the testes. In *Periophthalmus*, which comes from a tropical climate and which is not a periodic spawner, he found that the secretions are present throughout the year. Although *Gillichthys* is a periodic spawner, the seminal vesicles contain approximately the same amount of fluid and the secretory cells have the same appearance at all seasons. Directly after the act of spawning has been completed, however, the vesicles contain less fluid as it is largely expelled as a constituent of the milt.

#### SUMMARY

1. The mudsucker, *Gillichthys mirabilis*, has well developed seminal vesicles. These accessory sexual organs are specialized portions of the posterior end of the testes, and are not homologous with the seminal vesicles of higher vertebrates. The function of the vesicle is not known.

2. The vesicular contents maintain the sperm in viable but inactive condition. Activation is probably effected by a change in osmotic pressure. Maintenance of the spermatozoa may be the function of the vesicles.

3. The testes are simple in structure and comparatively very small. The germinal elements are contained in sac-like lobules, each of which empties directly into a dorsal spermatic duct.

4. No seasonal changes were observed in the seminal vesicles. On the average, the height of the epithelial cells and the location of the nuclei seem to remain constant. The vesicles contain most fluid in the post-spawning month of September. The amount of fluid is small during the breeding season because much is expelled by spawning.

5. The testes undergo a seasonal cycle. Except when emptied by the spawning act, the lobules are packed with spermatozoa during the breeding season, January to July. In August and September, cysts of spermatocytes and spermatids increase in number, and few spermatozoa remain in the lumen of the lobules. By November, the spermatozoa for the next spawning period are being produced, and the cysts of germ-cells decrease in number.

6. Methyl testosterone added to the water and injected into the fish and nonesterified testosterone added to the water apparently have no effect on the seminal vesicles. The epithelial cells and the fluid contents remain unchanged. This fact shows that the seminal vesicles of *Gillichthys* differ

from those of higher vertebrates physiologically as well as in embryonic origin.

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## Body Length of the Smallmouth Bass at Scale Formation

By W. HARRY EVERHART

THE body length at scale formation has been the cause of much discussion since the proposal by Fraser (1916) advocating its use as the correction factor in the formula for the back-calculation of lengths. Consequently the body length at scale formation and the subsequent development of the scale pattern were determined by observation for the smallmouth bass, *Micropterus dolomieu* Lacépède.

Klaatsch (1890) described the scales of the brown trout, *Salmo trutta* Linnaeus, as appearing in the anterior and median region of the trunk near the lateral line and then spreading caudad, ventrad, and dorsad from this region. Tims (1906) stated that scales first appeared in the Gadidae at a total length between 3 and 4 cm. Fraser (1916) working with the king salmon, *Oncorhynchus tshawytscha* (Walbaum), found that the total length averaged 2 inches at time of scale appearance and used that figure as the correction factor in his formula for back-calculating body lengths from the scale. Working on the scale order of the herring, *Clupea harengus* Lin-

naeus, Huntsman (1919) found when the total scale length and total body length were plotted they gave a length of 45 mm. as the length of the fish when the scales were first laid down. This length of 45 mm. at scale formation agreed with the actual observations. Huntsman further stated that the scales of the gray squeteague, *Cynoscion regalis* (Cuvier and Valenciennes), appeared at a total length of 30 to 40 mm. and of the alewife, *Pomolobus pseudoharengus* (Wilson), at a total length of 28 mm. The scales of the Atlantic herring and alewife (Huntsman, 1919) first appeared along the lateral line between the anal and caudal fins and from this point the scaled area extended predominantly forwards, more slowly backwards, downwards and upwards. Potter (1925) found that the scales of the bluegill, *Lepomis m. macrochirus* Rafinesque, made their appearance at a standard length of 17 mm., with the scales scattered over the anterior part of the body. Working with a miscellaneous collection of coregonid juveniles, Van Oosten (1929) concluded that the total length of both the lake herring and the whitefish at scale formation was approximately 35 to 40 mm. Parrott (1933), working with the brown trout, *Salmo trutta*, agreed with Paget (1920) that his data indicated that the standard length of the fish when the scales first appeared averaged approximately 35 mm. The scales were first observed along the lateral line slightly posterior to the dorsal fin. From this area they developed in an anterior and posterior direction along the lateral line and at the same time spread dorsally and ventrally. Setna (1934), working also with brown trout, confirmed the results of Paget and Parrott, finding that the scales first appeared along the lateral line at a standard length of 30 mm. Elson (1939), studying the brook trout, *Salvelinus fontinalis* (Mitchill), found that at a standard length of 36 mm. the scales extended dorsally and ventrally from the lateral line, and that trout of 40 mm. have scales showing sufficient growth to imbricate, and finally that fish of 59 mm. are entirely covered with scales. Brown (1943) reported that the smallest specimen of Montana grayling, *Thymallus signifer montanus* (Richardson), with scales was 35.5 mm. in total length. In older specimens the lateral line scales and those immediately above and below had more circuli than those near the dorsal and ventral region. Robertson (1947), in measuring 81 Yellowstone cutthroat trout, *Salmo clarkii lewisi* (Girard), reported that the scales first appeared on an average at a total length of 46 mm., but that there was considerable variation between individual fish.

#### MATERIALS AND METHODS

Bass for the work on the determination of the body length<sup>1</sup> at time of scale formation were obtained from the 1946 smallmouth bass stock raised at the Cornell Experimental Hatchery. The adult breeders had been taken from Cayuga Lake, New York. The bass were hatched and raised in a quarter-acre pond. Hatching occurred on May 26 and, beginning June 26, weekly samples were taken until August 8, 1946.

Fork length of all specimens was determined by measuring to the nearest millimeter with dividers.

<sup>1</sup> Original measurements on all fish included standard length, fork length, and total length. Average conversion factors for lengths on these fish were computed as follows: fork length  $\times 0.88$  equals standard length, and fork length  $\times 1.04$  equals total length.

The fish were skinned following the method employed by Neave (1943). Incisions were made with a razor blade along the back, belly and around the gill region. The skin was then stripped from the specimen. Except where one or the other side was damaged both sides were mounted.

Hollister (1934) was consulted for the staining technique. The skins were stained in alizarin red and mounted permanently in balsam.

The high power of a compound microscope was employed in determining the first appearance of the scales. For obtaining the scale pattern the slides of the skins were projected at a magnification of 40X using a Bausch and Lomb microprojector and the image traced on graph paper.

### RESULTS

*Body length at time of scale formation.* An examination of over 200 slides of bass ranging from 16 mm. to 46 mm. yielded mounts of 30 in which the scales were just visible. The scales were considered just visible or formed when only the first circulus around the platelet was stained. The mean length of these 30 bass whose scales had just formed was  $20.2 \pm 1$  mm.

Table I gives a frequency distribution of the bass with the scales just formed and those on which scales had not developed. The range of the 30 specimens on which the scales has just formed was from 18 mm. to 23 mm. Thirteen of all the mounts, within the mean length plus or minus one standard deviation, were without scales. Although 77 slides were examined of fish

TABLE I

FREQUENCY DISTRIBUTION IN ONE-MILLIMETER CLASSES OF YOUNG SMALLMOUTH BASS BETWEEN THE LENGTHS OF 16 MM. AND 23 MM. WITHOUT SCALES AND WITH THE SCALES JUST FORMED.

Class in mm.	Without scales	With scales just formed
16	2	0
17	4	0
18	6	1
19	10	14
20	3	8
21	3	5
22	0	1
23	1	1

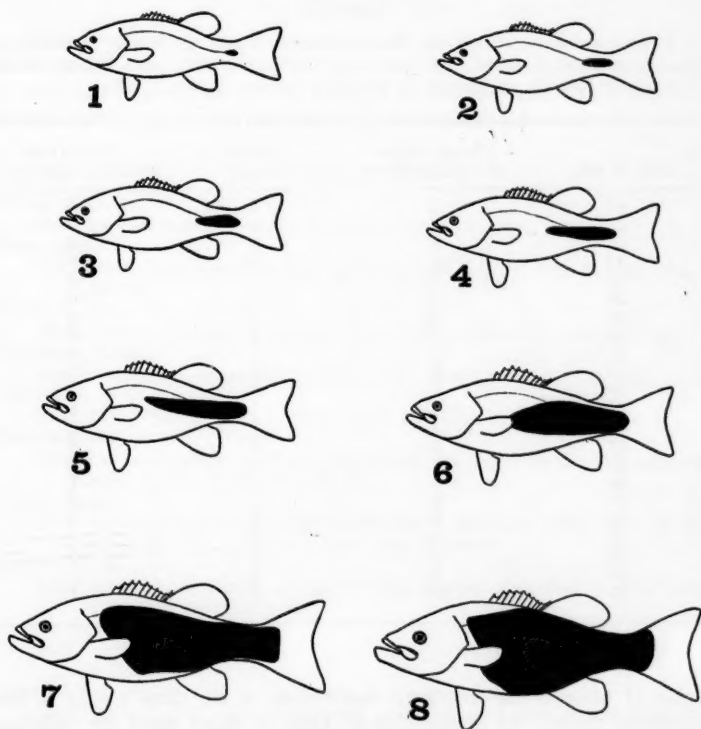
with fork lengths from 24 mm. to 45 mm., none was discovered without scales or with the scales just formed. All bass above 24 mm. had scales too far advanced to be included in either of the categories set up in Table I.

The overlap between those bass without scales and those with the scales just formed is evident. This wide variation is in keeping with results of other workers cited above. The data at hand indicate that the majority of bass with the scales just formed varied from 19 to 22 mm. Bass below 19 mm. may be expected to be largely unscaled.

*Origin and development of the scale pattern.* Figs. 1-8 show diagrammatically the location of the origin of the scales and the subsequent develop-

ment of the scale pattern. The specimens used in the illustration were chosen as typical representatives of the stage in the development which they demonstrate.

The scales first arose on the caudal peduncle just anterior to the caudal fin along the lateral line. From here the scales spread predominantly anteriorly, less rapidly dorsally and ventrally, and least rapidly caudally.



Figs. 1-8. Diagrammatic representation of young smallmouth bass showing origin of scales and development of scale pattern. Enlarged 1.5X. Lengths of bass were as follows: Fig. 1, 21.0 mm.; Fig. 2, 21.6 mm.; Fig. 3, 21.9 mm.; Fig. 4, 23.0 mm.; Fig. 5, 24.9 mm.; Fig. 6, 26.1 mm.; Fig. 7, 31.1 mm.; and Fig. 8, 32.0 mm.

Since the scales arose on the caudal peduncle and then spread anteriorly, some criterion was needed to determine the body increment necessary from the length at the time of formation of the caudal scales until the pectoral scale had developed. Consequently a count of circuli of both the caudal scales and the pectoral scales was made, dividing the fish into three groups. The first group, with an average fork length of  $24.5 \pm 3.3$  mm. ( $n=53$ ), had a greater number of circuli on the scales in the caudal region than on the scales



in the pectoral region. The second group, with an average length of  $29.8 \pm 3.4$  mm. ( $n=32$ ), demonstrated an equal number of circuli on scales from the caudal and pectoral regions. The third group, with an average length of  $33.8 \pm 3.7$  mm. ( $n=25$ ), contained those fish which had one more circulus on the pectoral scale than on the scale from the caudal region.

TABLE II

FREQUENCY DISTRIBUTION OF ONE-MILLIMETER CLASS OF YOUNG SMALLMOUTH BASS BETWEEN THE LENGTHS OF 19 MM. AND 45 MM. CLASSIFIED WITH RESPECT TO THE COMPARATIVE NUMBER OF CIRCULI ON THE PECTORAL AND CAUDAL SCALES

Class in mm.	Circuli greater on caudal scale	Circuli equal	Circuli one greater on pectoral
19	1	0	0
20	1	0	0
21	6	0	0
22	10	0	0
23	7	1	0
24	9	3	0
25	8	3	0
26	3	4	0
27	2	2	0
28	0	0	0
29	1	2	2
30	2	2	5
31	0	1	2
32	2	5	3
33	1	4	3
34	0	2	1
35	0	2	2
36	0	1	3
37	0	0	1
38	0	0	0
39	0	0	2
45	0	0	1

Table II presents the frequency distribution of the three groups in one-millimeter classes. An examination of Table II shows again the individual variation first observed in the length at scale formation. The general trend of the data is towards the greater number of circuli in the pectoral scales with an increase in body length. Furthermore, even though the scales arise on the caudal peduncle, only a small increase in body length is necessary before the pectoral scales have surpassed the caudal scales in development of circuli.

## SUMMARY

Weekly samples of young smallmouth bass were taken from a hatchery pond. After measuring and skinning, the skins were stained with alizarin red. From an examination of the stained skins scale formation was first observed at an average fork length of  $20.2 \pm 1.0$  mm.



Development of the scale pattern was examined by projecting the skins and tracing the outline of the region in which the scales had formed. It was determined that the scales first arise on the caudal peduncle just anterior to the caudal fin along the lateral line. From this beginning the scales spread predominantly anteriorly, less rapidly dorsally and ventrally, and least rapidly caudally.

#### ACKNOWLEDGMENTS

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## The Systematic Status of *Plethopsis* with a Discussion of Speciation in the Genus *Batrachoseps*

By ROBERT C. STEBBINS and CHARLES H. LOWE, JR.

BISHOP (1937) reported the discovery of a new plethodontid salamander in Oregon. He established for this form the genus, *Plethopsis*, so named because of its resemblance to *Plethodon*. Regarding the relationships of *Plethopsis*, Bishop writes:

This genus is related to *Plethodon* from which it differs in having only four toes, vomerine and parasphenoid teeth often forming a continuous series, incompletely ossified parietals and frontals and multiple testes in large males. From *Hemidactylum* it differs in lacking the basal constriction of the tail, in the condition of the parietals and frontals, in the number of costal grooves, the multiple testes and the lack of a marked sexual dimorphism. It resembles *Batrachoseps* in the incompletely ossified parietals and frontals but differs in the possession of two premaxillae, larger hind limbs, in the number and disposition of the teeth, multiple testes and lack of worm-like body.

On April 21, 1948, we secured individuals of *Plethopsis wrighti* at the type locality, 8.7 miles southeast of Sandy, Clackamas County, Oregon, and at Cherryville, Clackamas County. We failed to find the animals at the third reported locality, Middle Santiam River, Linn County, Oregon. Upon seeing this species alive and in its natural setting, we were impressed with its resemblance to *Batrachoseps*. In view of this similarity we have undertaken a comparative study of *Plethopsis*, *Plethodon*, and *Batrachoseps*, the results of which are reported here.

For several months we have had in the laboratory living *Plethopsis*. An adult female was induced to lay eggs by employing the technique of whole pituitary transplantation, used with such success by Noble and Richards (1930). Living *Batrachoseps attenuatus* from several localities in California have been employed in comparisons of structure, pigmentation, and behavior, and freshly laid eggs of this species have been compared with those of *Plethopsis*. We also have had available abundant preserved material of *Batrachoseps*, including representatives of all the currently recognized forms of the genus. Nine skeletons of *Batrachoseps* and two of *Plethopsis*, stained with alizarin red, have been used in skeletal analyses. At the same time we have had on hand preserved specimens of nearly all the species of the genus *Plethodon* and alizarin-stained skeletons of several of these. We have had available living representatives of all the species of this genus in western North America. Using pituitary transplants we have obtained the eggs of *Plethodon dunni* and *P. vehiculum*.

In our analysis, we have not felt it necessary to include *Hemidactylum*. Although this genus has in common with *Plethopsis* four toes on the hind feet, it differs considerably in having an aquatic larval stage, a characteristic that tends to set it off from many other plethodontids. In discussing the affinities of *Plethopsis* then, we have confined ourselves to comparisons with *Batrachoseps* and *Plethodon*.

Before proceeding further it should be stated that, contrary to the opinion of Bishop (1943) and Hilton (1946), we recognize 2 species in the genus

*Batrachoseps*. We follow Campbell (1931: 133) in recognizing a larger lighter-colored form of the islands and mainland of southern California as specifically distinct from *B. attenuatus*. In support of the distinctness of these forms, Campbell (1931) notes that *major*<sup>1</sup> and *attenuatus* have been found together in South Pasadena along the Arroyo Seco and that *pacificus* and *attenuatus* have been taken together on Santa Cruz Island. On morphological grounds, Campbell includes *major* with the insular forms, *catalinae* and *pacificus*. Both of the latter have at one time been considered species in their own right. He notes that *pacificus* (the form on Santa Cruz, Santa Rosa, and San Miguel islands) resembles *major* so closely that the two cannot be told apart with much certainty. Salamanders of the *pacificus* complex differ from *attenuatus* principally in having a more *Plethodon*-like habitus—that is a shorter and broader body, broader head, less reduced limbs, and longer toes. They differ further in being generally lighter colored. This may be noted particularly on the ventral surfaces, where the melanophores commonly appear as punctations, whereas in *B. attenuatus* a close network is formed. This, however, is not an absolute difference between the two species since some individuals, particularly young *pacificus*, may be nearly as dark ventrally as *attenuatus*. We view *pacificus* as a relic type, preserved on the Channel Islands and at a few localities on the adjoining mainland of southern California.

The existence of *Batrachoseps attenuatus caudatus* in southeastern Alaska requires confirmation. The species has not been found between this area and southwestern Oregon. Only the type specimen of *caudatus*, described by Cope (1889) as a distinct species, is known. The type seems to differ clearly in no way from *attenuatus*. The long tail, comprising 62.2 per cent of the total length, the character upon which the name is based, is equalled in occasional larger individuals of *Batrachoseps attenuatus*. This form may be based on a mislabelled specimen.

#### COMPARISONS

**STRUCTURE.**—In our opinion the habitus of *Plethopsis* is closer to *Batrachoseps* than it is to *Plethodon*, as we believe Plate I depicts. To illustrate the genus *Plethodon*, we have chosen *P. cinereus*, a moderately attenuate species. Note particularly differences in the head region—the relatively larger eyes, blunter snout, and narrowing of the head behind the eyes in *Plethopsis*, traits shared with *Batrachoseps* but which tend to set off *Plethopsis* and *Batrachoseps* from *Plethodon*. The shape of the head behind the eyes is largely due to the configuration and position of the epibranchial cartilage. In *Plethodon*, as based on dissection of *P. cinereus* and *P. vehiculum*, this cartilage is shorter, more curved, and extends more sharply laterally than in *Plethopsis* or *Batrachoseps* (Figs. 16–19). Further, *Plethodon* seems to differ rather consistently from these genera in the configuration of the furrows marking the skin of the head and neck. *Plethodon cinereus* is representative in this regard. In relative length of limbs and digits, differences between *Plethopsis* and *Batrachoseps attenuatus* are bridged by *Batrachoseps pacificus*.

<sup>1</sup> This form has been variously treated—as a species in itself, a race of *attenuatus* (Bishop, 1943) and, by Campbell, as a subspecies of *pacificus*.

Bishop gives costal grooves in *Plethopsis* as 16 or 17, counting one each in axilla and groin. Using his figures for the various forms of *Batrachoseps*, the range is from 17 (subspecies *pacificus*) to 21 (race *attenuatus*), again *B. pacificus* bridging the difference between *Plethopsis* and *B. attenuatus*. Inter-costal folds between tips of the toes of the appressed limbs are given as  $6\frac{1}{2}$ -7 for *Plethopsis* and for *Batrachoseps* range from 8 (*leucopus*) to 13 (*catalinae*). *Plethodon* ranges from 1 or less to 10 (*richmondi*). With the exception of 3 of the 17 species of *Plethodon* mentioned by Bishop (1943), all average fewer intercostal folds between the tips of the toes of the appressed limbs than in *Plethopsis*. *Plethopsis* thus falls roughly between *Plethodon* and *Batrachoseps* in this character.

In total length, on the basis of Bishop's averages, *Plethopsis* lies between *Batrachoseps attenuatus* and *B. pacificus*. It appears that in relative tail length, it does not differ notably from the others, although it does not seem to reach the lengths of some individuals of the species of *Batrachoseps*. See Table I for a comparison of characters between the forms of *Batrachoseps* and *Plethopsis*.

The feet of *Plethopsis* and *Batrachoseps* are similar in structure (Figs. 6-8). Both genera differ from *Plethodon* in possessing 4 rather than 5 toes on the hind foot. They correspond in number of joints in the digits. *Batrachoseps attenuatus* has considerably shorter toes than *Plethopsis* but *B. pacificus* bridges the difference, being perhaps somewhat closer to *Plethopsis* in this character.

In skeletal structure the 2 genera (*Batrachoseps* and *Plethopsis*) are much alike. They differ, however, in the character of the premaxilla. *Batrachoseps* possesses a single premaxillary bone; *Plethopsis* two premaxillary elements (Figs. 12 and 14). However, in 4 of the 20 *Batrachoseps* skulls studied, the nasal spines of the premaxillary element were separated.<sup>2</sup> Three of these were nearly full grown animals.

Number and disposition of the teeth are given by Bishop as differing between the two genera. There is a tendency in *Plethopsis* toward longer and more regular vomerine series and a greater tendency toward a juncture between the vomerine and parasphenoid tooth patches than in *Batrachoseps*. However, *B. p. pacificus* often has the vomerine teeth in series, and 2 of 12 *major* examined by us had the vomerine and parasphenoid teeth connected on one side. Hence, again we find the differences are not absolute. The parasphenoid patches may be separated, partly connected, or wholly united in *Batrachoseps*. In *Plethopsis* they are apparently rather consistently separated.

Dissection of the head and neck musculature in *Plethopsis*, *Batrachoseps attenuatus*, and two species of *Plethodon* (*vehiculum* and *cinereus*) has demonstrated no significant differences in myology, although we did not carry this analysis to the point of checking muscle insertions and origins. Those muscles studied corresponded with one another in shape and position although minor differences in proportions were noted.

Visceral structures were given a cursory examination. The position and

<sup>2</sup> Dunn (1926: 224) says the nasal spines are unfused in *Batrachoseps*. In the material examined by us from the vicinity of Berkeley, California, these processes were commonly firmly joined (Plate I, Fig. 14).

TABLE I  
(Data derived principally from Bishop, 1943)

	Costal grooves	Intercostal folds between tips of toes of appressed limbs	Intercostal folds over- lapped by hind leg when appressed to side	Total length (average in mm.)	Tail length percentage of total length	Vomerine teeth
<i>Batrachoseps attenuatus</i>	18-21(20)	10 -12½	3 -3½	89 (73 -114)	53.7-58.1	8-16
<i>    attenuatus</i>	18-20(19)	8 -11	4 -4½	87 (66 -127)	50 -62.2	5-8
<i>Batrachoseps leucopus</i>						
<i>    pacificus</i>	17-20(19)	9 -11	5½-6½	96.5(72 -129)	44 -54.3	7-10
<i>    pacificus</i>	20-21	10 -13	3½-4½	105.7(79 -133)	53.2-60.3	6-7
<i>    catalinae</i>	18-20(19)	9 -10	4 -4½	117 (82.7-162)	52 -57	7-11
<i>    major</i>						
<i>Plethopsis wrightii</i>	16-17	6½-7	4½-5	91.6(84 - 97)	51.8 (average of 3 ♂♂ and 3 ♀♀ lumped)	8-15

general shape of the liver, stomach, spleen, intestine, and reproductive organs seemed to be essentially the same in the three genera.<sup>3</sup>

The occurrence (in *Plethopsis*) of multiple testes in large adult males is occasionally observed in *Batrachoseps attenuatus* although the testes are usually single in this species. In the 3 genera the lining of the body cavity was noted as being suffused with dark pigment.

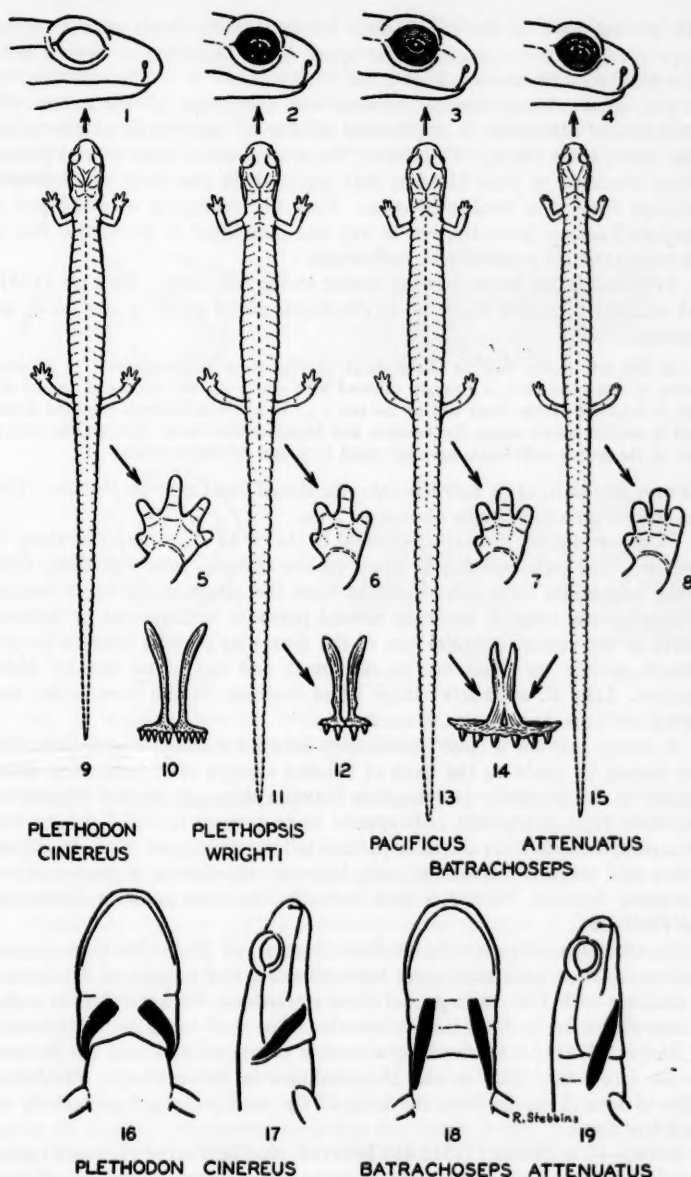
BLOOD.—Emmel (1924) pointed out that 95 per cent (range, 90–98 per cent) of the circulating erythrocytes of *Batrachoseps attenuatus* are non-nucleated. He also examined several individuals of *Batrachoseps pacificus* (*pacificus* and *major*) and found a similar blood picture. In contrast we find the erythrocytes of *Plethopsis* are largely nucleated, similar in this respect to the usual condition in amphibians. The blood difference, while marked, is not absolute since some of the red cells in *Batrachoseps* possess nuclei and about 6 per cent (based on a count of 300 erythrocytes in one individual) of the erythrocytes in *Plethopsis* are erythroplastids (non-nucleate). Incidentally, erythroplastids were found in 10 of the 11 urodeles studied by Emmel, the percentage being highest in the lungless species. *Plethodon oregonensis* [= *Ensatina eschscholtzii*] had the highest percentage (5.7 per cent) among the lungless types studied.

PIGMENTATION.—A comparison is made below between an adult *Plethopsis wrighti* from the type locality and an adult *Batrachoseps attenuatus* from 10.6 miles west of Dyerville, by road to Honeydew, Humboldt County, California. Both animals were alive when studied, anesthetized with chlorotone. This comparison may be considered representative for the forms considered.

In both species the dorsal band broadens on the head to include the upper eyelids, brightening on the tail. The band is similar in width. In both it apparently consists of guanophores, golden in color, overlain by reddish pigment. The dorsal band in the specimen of *B. attenuatus* differs in possessing a few scattered whitish guanophores, in a tendency toward grouping of the pigment cells to form short longitudinal streaks, and in weakening of the color on the head and neck with a tendency toward retention of the color of the dorsal stripe as a nuchal spot. Both species possess pale bluish-white guanophores on the lower sides. These give way to a fine stippling of golden chromatophores on the upper sides which do not extend to the dorsal band. Hence the dorsal band is margined by black or deep brown. In *B. attenuatus* the ground color of the sides is slightly less intense black and the whitish guanophores, rather uniformly distributed, occur largely singly or in small groups, not forming large blotches as in *Plethopsis*. In both animals a close reticulum of melanophores is present on the ventral surfaces although again the ground color in *Plethopsis* is deeper black. In both forms the ventral color lightens in the gular area. The color of the guanophores is similar in the two species but, as on the sides, they form larger groupings in *Plethopsis*, resulting in conspicuous whitish spotting in contrast to the whitish stippling of *attenuatus*. Pigment of the melanophores seems to be reduced beneath these white patches in *Plethopsis*. In both animals guanophores become less abundant along the midline. The limbs are similar in coloration in the two species but larger groupings of guanophores are present in *Plethopsis*.

<sup>3</sup> The two species *Plethodon cinereus* and *P. vehiculum* were again used to represent the genus *Plethodon*.





Figs. 1-19. Structural characteristics of *Plethodon*, *Plethopsis*, and *Batrachoseps*.

Figs. 1, 5, 9, 10, 16, and 17 are of *Plethodon cinereus*; Figs. 2, 6, 11, and 12 are of *Plethopsis wrighti*; Figs. 3, 7, and 13 are of *Batrachoseps pacificus major*; and Figs. 4, 8, 15, 18, and 19 are of *B. attenuatus attenuatus*. The items figured are as follows: Figs. 1 to 4—differences in length of snout and 2 to 4—variation in abundance of guanophores of the iris; Figs. 5 to 8—right hind foot in dorsal aspect; Figs. 10, 12, and 14—premaxillary bones; Figs. 9, 11, 13, and 15—habitus (animals all drawn with same snout-vent measurement to show differences in proportions); Figs. 16 to 19—position and shape of the epibranchial cartilages.

The ground color of the iris is deep brown in both forms with scattered coppery colored guanophores in the upper half. These are somewhat more abundant in *B. attenuatus* (Figs. 2 and 4).

The close correspondence between the coloration of *Plethopsis* and *Batrachoseps attenuatus* is emphasized further by individuals of *attenuatus* from Santa Cruz County, California. These were noted with ventral guanophores clustered to form blotches that approach in size those of *Plethopsis* although they were weaker in color. Thus the coloration of *Plethopsis* is duplicated almost perfectly, not in any one individual of *attenuatus* but in the color traits of a number of individuals.

Variation in the dorsal band is similar in the two forms. Bishop's (1937: 94) remarks regarding the band in *Plethopsis* could apply as well to *B. attenuatus*:

In life this species has the dorsal band varying from bright chestnut to reddish-brown, in some the band is strongly suffused with dusky on the snout and trunk; the band is brightest on the basal half of the tail. . . . In a few individuals the light dorsal band is reddish-brown along the margins and blotched with black through the center. Two of the largest individuals have the band very dull brownish-yellow.

We may add that, as in *Batrachoseps*, the dorsal band may be obscure. This was true of an adult female obtained by us.

In pigmentation *Plethopsis wrighti* is closer to *B. attenuatus* than *B. pacificus*. The latter species, as based on live material from Pasadena, California, and Santa Cruz Island, differs from the others in having a weaker melanic ground color, a tendency toward punctate arrangement of melanophores of the venter, essential loss of the dorsal stripe with increase in size (except usually for remnants on the snout and tail), and heavier iridic guanism. Like *B. attenuatus* large white blotches on the lower sides and ventral surfaces do not seem to occur.

A strong case for a close relationship between *Plethopsis* and *Batrachoseps* cannot be made on the basis of broader aspects of pigmentation alone because of the similarity in coloration between these genera and *Plethodon*. The same type of pigment cells appear to be present in the 3 genera and the arrangement to form the color pattern follows a common plan. In details of hue and arrangement of the cells, however, we observe a greater correspondence between *Plethopsis* and *Batrachoseps* than between *Plethopsis* and *Plethodon*.

**SEXUAL DIMORPHISM.**—As in *Batrachoseps* and *Plethodon* there appear to be no marked color differences between males and females of *Plethopsis*. In common with *Batrachoseps* and some plethodons, the lower jaw in males is somewhat more pointed than in females. The vent in males, as indicated by Bishop (1943), is bordered by a narrow depressed area and the lips are thrown into folds. This is also the condition in *Batrachoseps*. *Plethodon* males of several species have the folds of the vent prolonged posteriorly as short free flaps.

**EGGS.**—If, as Noble (1931: 48) believed, modification of eggs and larvae may be taken as providing evidence as to the affinities of species of amphibians, we may view the structure and manner of deposition of the eggs in *Plethopsis* as indicative of a closer relationship to *Batrachoseps* than *Plethodon*. Figure 20 gives relative size, number of jelly layers, and relationship



to one another in the clutch, of the eggs of *Plethodon vehiculum* and *Plethopsis wrighti*. The eggs of *Plethopsis* were laid in a rosary-like string, an arrangement found in *Batrachoseps* but not to our knowledge known for *Plethodon*. Twelve eggs were deposited. Eggs of *Plethodon* may be broadly adherent to one another and to the substratum or may be arranged like a cluster of grapes and attached by a common pedicel to the roof of the cavity chosen for a nest.

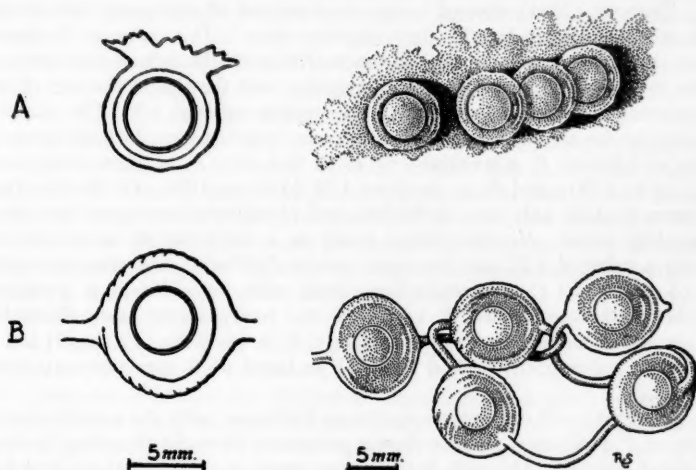


Fig. 20. Eggs of *Plethodon vehiculum* (A) and *Plethopsis wrighti* (B) showing jelly envelopes, manner of attachment, and arrangement in the clutch.

Emmel (1924) describes the gill of developing *Batrachoseps attenuatus* as "a . . . simple, slender, three fingered . . . structure, traversed by a single vascular loop for each finger-like process." *Plethopsis* larvae under our observation, on the other hand, possess large plate-like gills with a more extensive vacularization than in *Batrachoseps*.

BEHAVIOR.—Bishop (1937) comments on the position of *Plethopsis* when discovered in the field, "some specimens when found were coiled in a close spiral with the head held much like that of a snake." It was this posture along with the attenuate form that led us to view our first specimen as *Batrachoseps*. The characteristic watch-spring coil of *Batrachoseps* is familiar to all acquainted with this salamander in the field. So far as we know, this pose is not commonly assumed by any *Plethodon*.

It is a familiar experience in collecting *Batrachoseps* to observe a violent series of flipping movements involving the entire body. These contortions often throw the animal into the air. Following the thrashings, the individual may lie motionless, showing no outward sign of life. This reaction is likely to take place when an individual is first picked up. We noted nearly identical behavior in one of the *Plethopsis* secured.

The locomotion of *Plethopsis* and *Batrachoseps* is much alike. Peabody

(1941: 7) describes the locomotion of *Batrachoseps* as to carriage of the body as "... somewhat comparable to two men walking in line carrying a long pole between them." This essentially applies as well to *Plethopsis* although slight lateral undulations of the body may occur. *Plethodons* studied (*elongatus*, *vehiculum*, *dunni*, and *vandykei*), on the other hand, tend to move the body in marked lateral undulations when crawling, the difference probably stemming primarily from differences in ratio of limb to body length.

Peabody (1941) devised a numerical method of expressing limb length in relation to body length—the "coupling value." This value is the gleno-acetabular (or axilla to groin) distance divided by the sum of the length of the fore and hind limb. Thus a salamander, with the tips of the toes of the appressed limbs meeting, would have a coupling value of 1.00. The coupling value for the several forms of *Batrachoseps* compiled from Peabody's report are as follows: *B. attenuatus* 2.67 (2.20 to 3.16); *B. pacificus major* 2.14 (1.92 to 2.38); and *B. p. pacificus* 1.75 (1.43 to 2.00). Of all the other genera studied, only two plethodons and *Hemidactylium* range into these coupling values—*Hemidactylium*, based on a single set of measurements, with a value of 1.77 and the single species *Plethodon elongatus*, averaging 1.63 (1.49 to 1.85), corresponding closely with *Batrachoseps p. pacificus*. Other plethodons studied, *P. vehiculum* and *vandykei*, are below *Batrachoseps* and *P. dunni* overlaps only slightly *B. p. pacificus*. *Plethopsis* has a coupling value of 1.70 (1.60 to 1.86) as based on 3 specimens measured by us.

**HABITAT.**—All our western species of *Plethodon*, with the possible exception of *P. vehiculum*, seem to show a preference for rocky situations in their habitat selection. Although *Batrachoseps* occurs in such situations, it is less characteristically found in rocky places. The conditions under which we obtained *Plethopsis* corresponded closely as to type of cover, soil moisture, leaf litter, and general aspect of the vegetation to those under which one encounters *Batrachoseps*. Individuals were found inside termite channels in rotten logs, where *Batrachoseps* also occurs. The slender form and small limbs of the two salamanders facilitate such occurrence.

#### SUMMARY AND CONCLUSIONS

*Plethopsis* agrees with *Plethodon* but differs from *Batrachoseps*, as far as our analysis goes, in at least two characteristics—in possessing a high percentage of nucleated erythrocytes and in having two premaxillary bones. It possesses multiple testes in large males, differing in this regard from both of the other genera, although this difference is not absolute so far as *Batrachoseps* is concerned. With *Batrachoseps*, however, it shares a considerable number of characteristics. These genera possess in common 4 toes on the hind foot, close correspondence in habitus, pigmentation, skeletal features (with the exception noted), character of the eggs, behavior, and habitat selection. In view of these facts a question is raised regarding the advisability of continuing its rank as a monotypic genus. Considering it as such means placing what is perhaps undue emphasis on the differences involved, resulting in obscuring the similarities between it and *Batrachoseps*. Its position as a monotypic genus might be more tenable in the absence of *Batra-*

*choseps pacificus*, which bridges (particularly through the race *pacificus*) dentitional differences and differences in proportions.

Since in *Plethopsis* and *Batrachoseps* there is similarity or overlap in all characters studied, except the condition of the premaxillae, the question regarding the status of *Plethopsis* seems to hinge on whether or not we shall consider this difference as sufficiently fundamental to form the basis of a separate genus. We consider *Plethopsis* as closely related to *Batrachoseps* and we propose that it be included in this genus. If so considered it would be viewed as a somewhat less specialized species than the others and might be considered ancestral to the other two (*pacificus* and *attenuatus*) or at least near the ancestral type. Both *P. wrighti* and *B. pacificus* appear as relic forms, more *Plethodon*-like in habitus than *attenuatus*. *Plethopsis wrighti* in its blood picture and paired premaxillae, in conjunction with other traits, bears features that suggest that it may have had a *Plethodon* or *Plethodon*-like ancestry, as Bishop intimated. It seems possible that at one time *pacificus* and *wrighti* were connected, although perhaps not in their present form, *attenuatus* being derived directly from *pacificus* or a common ancestral stock. In view of the extensive intra-specific variation in color and form in some other salamanders, such as *Ensatina eschscholtzii* and *Aneides flavipunctatus* (results of studies as yet unpublished), conjecture of such a connection does not seem unreasonable.

One can imagine how the present picture might have developed (Fig. 21). Envisage a homogeneous ancestral population oriented along a north-south axis, composed of a form like *Plethopsis*. Superimpose on this a selectional gradient to the south for more attenuate form, reduction of limbs and toes, greater rigidity of the snout, greater oxygen carrying capacity of the red cells and lightening of the pigmentation. Such character trends might be expected to appear with increasing temperatures and reduction in humidity along a north-south axis. Such environmental changes might have favored the development of fossorial behavior. Reduction and loss of limbs, attenuation of the body, and increased rigidity of the skull, are presumed accompaniments of such habits in certain other vertebrate groups. Reduction in availability of oxygen at higher temperatures and greater difficulty in providing a wet skin for its absorption might have placed a premium on the oxygen absorbing capacity of the blood. Or modification in vascularity of the skin accompanying changes in form may have reduced the effectiveness of the skin in respiration. Loss of nuclei from the erythrocytes would provide a means of increasing the efficiency of the blood in transporting oxygen. On the other hand, it is of course possible that the change in the blood picture preceded and, in fact, may have made possible peculiarities of form in these salamanders. Lightening of coloration might be expected in conformity with Gloger's Rule, although, of course, not necessarily directly due to the factor of humidity itself. Thus we can hypothesize the appearance in this ancestral population, induced by factors associated with increasing aridity to the south, of northern and southern differentiates like the present forms, *pacificus* and *wrighti*. With continuation of the trend making for this discontinuity, one can imagine a break occurring and gradual disappearance of populations less favorably situated, resulting in the present distribution. The southern form, *pacificus*, is preserved on the islands off the coast of California and at a few localities

fringing the Los Angeles coastal plain, areas in southern California tempered in climate by coastal fogs. The northern type, also a relic, exists in an area in Oregon that is in some obscure way particularly suited to its needs.

A *Batrachoseps* similar in size and limb length (coupling value of at least 2.20) to *B. pacificus major* existed in what is now the foothill area of the Sierra Nevada of California in Pliocene time, according to Peabody (1941). The occurrence of this animal is based on an analysis of fossil trackways found in the Buchanan Tunnel,  $1\frac{1}{2}$  miles west of Columbia, Tuolumne County, California. This discovery tends to bridge the geographical gap between *Plethopsis* and *Batrachoseps pacificus* and may be taken as support for the foregoing hypothesis of a previous distributional continuity.

A hypothesis for the derivation of *attenuatus* offers greater difficulty. It seems likely that it originated from *pacificus*, or at least passed through a *pacificus*-like stage in its development before reaching its present worm-like condition. In pigmentation, however, it would seem to be closer to the ancestral condition than present day *pacificus*. *B. attenuatus* today is clearly the widespread adaptable species. It must have secondarily invaded the range of *pacificus* since they are sympatric in southern California. Because it has carried farther the trends of body form observed in *pacificus*, we may conjecture that it developed in an area where still greater stress was placed on the evolution of this form. One possibility is that it evolved still farther south where Bergmann's Rule was reversed (for coldbloods) through selectional advantages of small size in escaping into the ground to avoid high temperatures and drying of the surface, or other advantages of such size and form. Gadow's (1905) record<sup>4</sup> for the species in the Nevada de Colima, Mexico, and its possible occurrence at La Paz, Lower California (Lockington, 1880), may be considered as in line with this theory. The La Paz record needs confirmation. A second possibility is that *attenuatus* differentiated somewhere to the north. If its size and pigmentation have been stable, they may be taken as supporting a northerly origin in keeping with both the rules of Bergmann and Gloger. Camp (1915: 229) reports that the localities of capture for *major* lie in the upper edge of the Lower Sonoran Life-zone (mesa oak association), below the range of *attenuatus*. The latter species appears to inhabit the Upper Sonoran Zone (maple-sycamore association) in the mountain canyons. This also has been our experience in collecting these salamanders. Such occurrence lends support to the view of a northerly origin if we assume a tendency in this group toward adherence to primordial habitat conditions. It appears likely that the Great Valley of California has long been a barrier to plethodontids. If true this would provide for separation of coastal and interior populations derived from the north. A *pacificus*-like form may have differentiated interiorly, as evidenced by the fossil trackways, eventually extending its range into southern California via the east side of the Great Valley. Concurrently, or at a later time *attenuatus*, differentiating coastally, may have dispersed southward to invade the range of *pacificus*. The terminal populations of the interior and coast, upon reaching southern California, had diverged genetically to such an extent that upon reaching southern California they had arrived at the species level in their relationships.

<sup>4</sup> The specimen collected by Gadow has been examined. We concur with his identification.

Since *attenuatus* at the northern extreme of its range seems to be no closer morphologically, in any clear way, to *Plethopsis* than individuals from farther south, it does not appear likely that there was ever a direct connection between *Plethopsis* and *attenuatus* in the area now separating these forms.

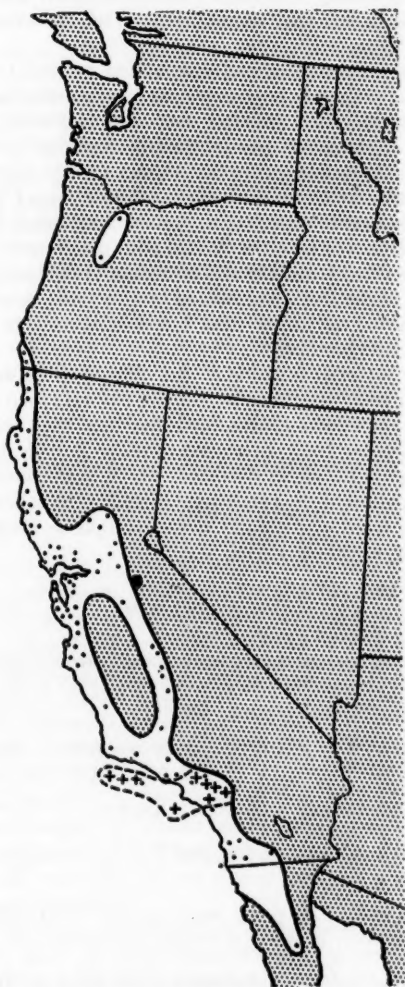


Fig. 21. Distribution of (1) *Plethopsis wrighti*, the small unstippled area in northwestern Oregon; (2) *Batrachoseps attenuatus*, principally in California, coastally and interiorly (the locality at Colima, Mexico is not shown); (3) *B. pacificus*, indicated by crosses (+); and (4) a fossil *Batrachoseps* allied to *B. pacificus*, indicated by the large black dot in east-central California in what is now the foothills of the Sierra Nevada.

*Plethopsis*, if ancestral to *attenuatus*, must be so indirectly through *pacificus* or a *pacificus*-like type. Hence it appears to us that *attenuatus* has dispersed northward, secondarily approaching the range of *Plethopsis*. Likewise, the scarcity of the species in the foothills of the Sierra Nevada of California and the apparent recent invasion of this area by several other plethodontids with which *attenuatus* is usually associated (*Aneides lugubris* and *Ensatina escholtzii*) cause us to feel that its occurrence there is secondary and relatively recent.

On the basis of pigmentation and distribution we tend to favor the view that from a coastal differentiation center, as for example the San Francisco Bay area, where the species is probably most abundant today, *attenuatus* has dispersed radially to the north, east, and south—ranging to the south as far as Colima, Mexico. It is noteworthy that Gadow (1905) viewed his find as a comparatively recent immigrant from the northwest, from California, and he believed it probable that the species . . . “occurs all through the slopes of the western Sierra Madre, which is mostly clad with pine forests.” If the dating of the fossil type is correct, and there is no reason to doubt it, and if *attenuatus* is a derivative of the stock represented by this type, then the events conjectured have occurred no earlier than Lower Pliocene and may well have taken place in Pleistocene time.

In view of the essential bridging of the differences between *wrighti* and *attenuatus* through *pacificus*, thus composing a natural group no more diverse than some other amphibian genera, and the fact that the characters of *wrighti* are not peculiar to it alone, we consider it desirable to recognize *wrighti* as a member of the genus *Batrachoseps*. A more inclusive and slightly broader characterization of the genus would include the following statement: premaxillary bones fused or separate; testes multiple or single; erythrocytes predominately with or without nuclei.

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## Bipedal Locomotion of the Lizard *Basiliscus basiliscus*<sup>1</sup>

By RICHARD C. SNYDER

THE literature of herpetology contains numerous references concerning bipedal locomotion in lizards. Cope (1875) mentions that *Basiliscus vittatus* runs over water in an upright position and de Vis (1884) states that the Australian agamid, *Chlamydosaurus kingi*, is plantigrade when running bipedally and that the angle of trunk inclination from the horizontal is about sixty degrees. Saville-Kent (1895) writes that the bipedal gait is the normal one for *Chlamydosaurus* when the lizard is traversing level ground for any distance, that the forelimbs hang lax and motionless, and that the tail is elevated and sways from side to side. Later (1898), he states that bipedal locomotion occurs in *Physignathus lesueuri*, *Amphibolurus muricatus*, and "to a lesser extent" in *Agama stellio*, *Ameiva surinamensis*, *Basiliscus basiliscus* (*americanus*) and *Tupinambis teguixin* (*Teguixin americana*). He suggests that such lizards, not closely related, have inherited this gait from the bipedal dinosaurs.

Several other references contain brief remarks on this type of locomotion. Gadow (1901: 523) pictures *Chlamydosaurus* sitting erect and using the tail base as a support, kangaroo fashion. Lydekker *et al* (1912: 95) dis-

<sup>1</sup>The writer is indebted to Dr. Harold Trapido, Gorgas Memorial Laboratory, Panama, who furnished the basilisk lizards; to Dr. A. A. Allen, Cornell University Laboratory of Ornithology, who took the strobilite photographs; and to Dr. P. W. Gilbert, Cornell University Zoology Department, who assisted with many phases of the work.

cuss bipedalism in both recent and primitive reptiles and correctly suggest that both stocks have developed the gait independently. Osborn (1916: 753) shows illustrations of *Physignathus* and *Chlamydosaurus* running on their hind legs and mentions that neither lizard appears able to rear off the ground unless high speed has previously been attained in quadrupedal running. Barbour (1926: 54) includes *Laemantus serratus* and *Deiropyx* sp. in the group of bipedal species. Burt (1931: 193) indicates the possibility that *Cnemidophorus tessellatus* may be at least partially bipedal at high speed. Fitzsimons (1943: 131) states that, when running swiftly, *Agama atra* raises the forepart of the body well off the ground so that the forelimbs barely touch. Böker (1935-37: 136) includes *Grammatophora* sp., *Kentropyx* sp., and *Dipsosaurus dorsalis* in the bipedal group, and Loveridge (1945) mentions that *Hydrosaurus marmorata* is bipedal and that *Calotes versicolor* is nearly so at high speed. Barbour (1926: 55) shows a photograph of *Callisaurus draconoides* running bipedally. Barrett (1931), Howell (1944), Romer (1945) and Swanson (1945) include brief discussions or descriptions of bipedal locomotion in lizards and Ditmars (1933) and Smith (1946: 172) describe the gait of *Crotaphytus c. collaris*.

From an examination of the above references, many of which are fragmentary with respect to bipedal lizards, and from correspondence with many herpetologists, it would appear that the following species have definitely been observed to resort to this type of gait: *Crotaphytus c. collaris*, *Basiliscus basiliscus*, *B. plumifrons*, *B. vittatus*, *Callisaurus draconoides*, *Chlamydosaurus kingi*, *Physignathus lesueuri* and *Hydrosaurus marmorata*. It is highly probable that other species of the polytypic genera are bipedal at times. Several other species exhibit tendencies toward this gait but until proof to the contrary is forthcoming they should be classed as "partially bipedal." These lizards include *Dipsosaurus dorsalis*, *Uma inornata* and, possibly, *Cnemidophorus tessellatus* and *Calotes versicolor*.

The genus *Basiliscus* embraces several striking species found in tropical Mexico, Central America and northern South America. They are remarkable not only for their rapid bipedal locomotion, but also for their extremely long, attenuated tail and the development of the powerful hind legs. The male reaches the greater size and, in contrast to the female, has a crest on the occiput and a large dorsal crest covering the back and the proximal two-thirds of the tail. This crest is supported by elongations of the neural spines. According to Ditmars (1933: 62) and other authors, these lizards are excellent climbers and jumpers and in the natural state they are decidedly arboreal, usually reposing on limbs or bushes overhanging water into which they dive when alarmed. When on the ground they are able to run on the hind legs alone at great speed but at a slower speed they revert to a quadrupedal gait.

Ruthven (1912: 315) has an excellent account of the habits of *Basiliscus vittatus* of Mexico. He writes, in part: "Where the stream or lagoon is narrow, it may cross it, and twice I observed frightened individuals rush across a deep stream ten to fifteen meters wide . . . In the ones observed to cross deep water, the hind feet were moved exactly as on the land, and so rapidly that the body could not sink, i. e., the animal literally ran through

the water on its hind legs . . . it was not apparent that the tail functioned to any degree as a rudder." These observations have been confirmed by the writer for *B. basiliscus*, although this lizard never ran on the water for more than two strides. Dr. Brayton Eddy, curator of reptiles at the New York Zoological Park, has recently taken motion pictures of *B. plumifrons* running on water and he has informed the writer (personal communication) that the lizard took two or three steps, then folded its front legs and dove. Once the feet were wet, it could no longer support itself upon the surface film. It is probable that unless these lizards attain considerable speed before reaching water, they are unable to cross it for any distance and that their momentum is as important a factor as the rapidity of action of the hind feet.

In the present work the locomotion of the basilisk was studied with the aid of high speed motion pictures taken at 64 frames per second as the lizard ran before a ruled grid background. The wooden running platform was covered with large sheets of coarse sandpaper which provided a rough friction surface and prevented backslipping. The entire platform was enclosed in a large glass tank providing visibility from every direction except from below. The lizards were then photographed through the glass from the lateral, anterior and posterior aspects. Individual frames of the motion picture were then projected and the outlines of the lizard traced throughout a complete locomotor cycle. The positions of the joints were determined on each tracing and the tracings were then superimposed, using the acetabulum as the central reference point. The inclinations of the body and the positions of the legs and tail in each phase of the stride were then plotted by means of a protractor.

No attempt was made to analyse the quadrupedal gait of *Basiliscus* since no illustrative slow-motion pictures were obtained. It is certain, however, that both walking and quadrupedal running are symmetrical forms of locomotion as Howell (1944: 224) has pointed out. The walking lizard has at least two legs in contact with the ground at the same time, a hind foot and the contralateral forefoot. Thus the left hind foot and the right forefoot are advanced nearly simultaneously and the support of the body shifts from one diagonal to the other. Howell noted that some lizards exhibited a modification of the walking gait in that the advancement of a hind foot followed, rather than paralleled, the action of the opposite forefoot. It was noticed that in *Basiliscus* the hind foot tended to advance slightly before the contralateral forefoot left the ground. This is probably due to the excessive length of the hind leg, which must be raised and advanced before its drag becomes too great.

The quadrupedal running gait of a lizard is difficult to compare with similar running gaits of mammals. In the former, the limbs are extended to the side and never, as in the majority of mammals, move primarily in the sagittal plane. The gait of *Basiliscus* is most closely comparable to the equine trot. However, unlike the trotting horse, in which appendicular support alternates from diagonal to diagonal, the hind foot of the lizard strikes the ground in advance of the opposite forefoot.

The position of the limbs in the resting *Basiliscus* is not unlike that of a frog. The hind legs extend forward and laterally with the shank flexed, and

the large hind feet rest flat on the ground in position for an immediate thrust. The forelegs are partially flexed and the forefeet are placed toward the midline of the body so that the anterior part of the body is raised well off the ground. The tail lies flat and motionless, although the lizard may switch the tip back and forth if alarmed or watchful. If the lizard is completely undisturbed, it may rest flat on its belly with the forelegs sprawled to the sides, but the position of the hind legs remains the same.

From either of the above mentioned resting postures, the lizard is able to rise at once to the bipedal position. Preliminary quadrupedal running may or may not precede the bipedal attitude. The forepart of the body is elevated and the forelegs are flexed so that they can no longer take part in locomotion. The proximal end of the tail is raised off the ground, although the tip may continue to touch. The initial forward thrust of the body is accomplished by the extension of both hind legs, but before the thrust is fully completed, one of the hind legs swings cranial in order to be in position to catch the descending body. Thus, the first stride of the lizard is initiated by one of the legs that first propels it forward.

The forelegs do not play an important role in elevating the body. These appendages were immobilized by taping them tightly to the animal's sides so that the basilisk was forced to rest flat on its belly and throat. From this position, it was able to rise without apparent difficulty and run on its hind legs. In the first trial it proceeded for two strides before falling forward on its belly, but after several trials it was able to run bipedally for the length of the experimental tank (5 feet). It seems evident that the elevation of the trunk is accomplished by the epaxial musculature of the back. The writer has twice noticed a captive adult male rear the forepart of the body while squatting in a resting position, and this attitude was maintained for several seconds while the lizard explored the top of the cage with his snout.

A complete locomotor cycle is illustrated in Figure 1. It will be noted that the basilisk raises the forepart of the body to its maximum height coincident with the initial forward thrust of the hind legs. The forelegs are partially flexed, the brachium extends laterally, and the base of the tail is raised from the ground (1). The right leg (in this case) is swung forward, and as it begins to extend (2), the body twists to the right due to the thrust of the left hind leg. The right hind foot strikes the ground in a plantigrade position (3) and, at the same time, the left leg begins its recovery. The right leg now bears the entire weight of the lizard (4) and as it begins to be retracted in the propulsive strike, the body rotates maximally to the right. At this period both thighs extend laterally, and a line passing from one knee joint through the acetabula to the opposite knee joint is approximately straight (Plate I, lower; Fig. 2, 2). The left foot now begins to dorsiflex as the recovery of the left leg proceeds, and as recovery is completed (5) the body begins to rotate toward the left, the tail base is elevated, and the right leg extends, propelling the body forward. The position of the right foot becomes digitigrade as the metatarsals flex on the digits. The angle of trunk inclination from the horizontal during this period decreases from approximately 46 to 31 degrees.

At this point the lizard begins to attain its maximum speed. The right

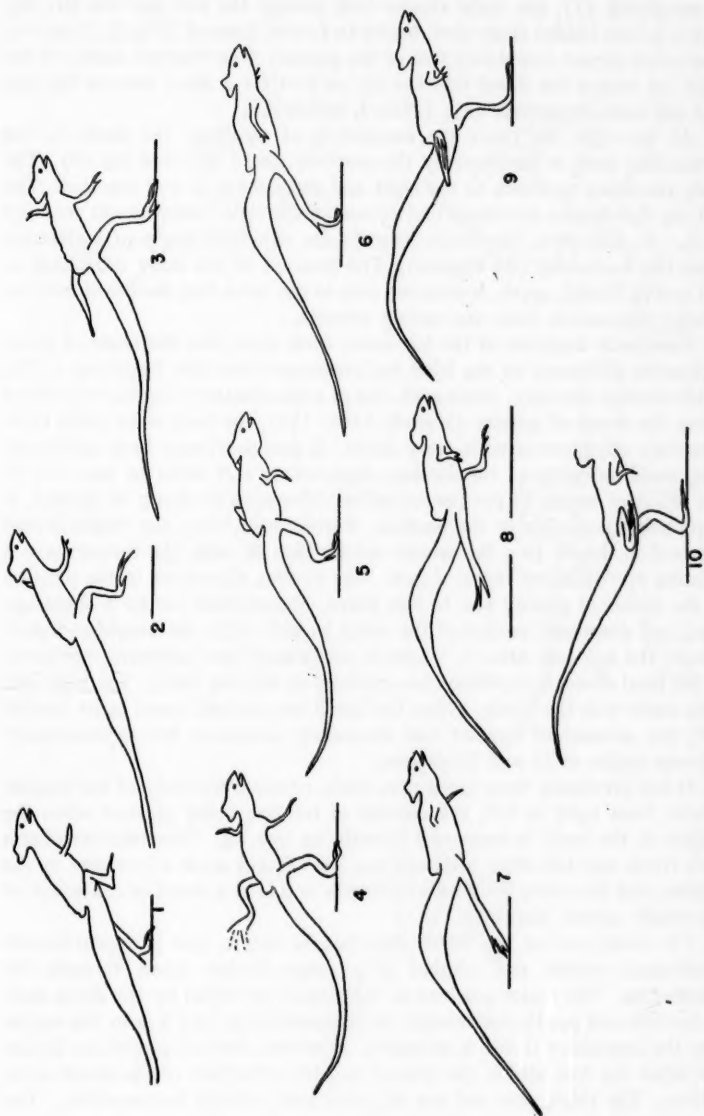


Fig. 1. Bipedal locomotion of *Basiliscus basiliscus*. Locomotor cycle in sequence 1-10. See text for discussion. Made from motion picture by projection; camera one foot above substrate.

leg continues to extend (6) and, simultaneously, the tail base is lifted far off the ground and the right foreleg swings caudad. As the propulsive thrust is completed (7), the body rotates well toward the left and the left leg, which is here hidden from view, begins to extend forward (Fig. 2, 3, and 4). The tail is almost completely free of the ground. The vigorous stroke of the right leg pushes the lizard into the air, so that for a short interval the feet and tail leave the ground (8): (Plate I, middle).

As the right leg nears the completion of recovery, the shock of the descending body is absorbed by the partially flexed left hind leg (9). The body continues to rotate to the right and the tail tip is well elevated. The left leg then begins to retract and extend as the right completes its recovery (10). At this time, the trunk assumes its minimum angle of inclination from the horizontal (20 degrees). The position of the body illustrated in (1) and in Plate I, upper, is observed only in the event that the lizard initiates bipedal locomotion from the resting position.

Composite diagrams of the locomotor cycle show that the angle of trunk inclination decreases as the hind leg progresses from the beginning of the stride through recovery. Since each step of a non-saltatory, bipedal vertebrate alters the center of gravity (Howell, 1944: 120), the body must make compensatory adjustments with every stride. It has previously been mentioned that some swinging of the forelegs does occur, and while in man this is the principal means of compensating for differences in center of gravity, it is probably negligible in the basilisk. Furthermore, since the thighs extend outward in lizards to a far greater extent than in man, the former have a twisting or "waddling" type of gait. The various alterations in the position of the center of gravity are, in this lizard, compensated for by a slight upward and downward motion of the trunk as well as by the weight and position of the tail (see below). There is no forward and backward movement of the head alone, a condition characteristic of walking birds. The head and neck move with the trunk. When the lizard has attained speed in its bipedal gait, the amount of upward and downward movement lies approximately between angles of 31 and 20 degrees.

It has previously been noted that, while running, the body of the basilisk rotates from right to left, the amount of rotation being greatest when the weight of the body is supported directly on one leg. This rotation affects both trunk and tail alike, although the head makes some adjustment to the motion, and the entire body rolls from side to side as a result of the action of the widely spread hind legs.

The distal end of the femur describes an ellipse that is approximately equidistant caudad and cranial of a perpendicular drawn through the acetabulum. The major portions of the ellipses described by the distal ends of the crus and pes lie posterior to the perpendicular, and it is in this region that the propulsive thrust is strongest. However, forward propulsion begins just after the foot strikes the ground and the retraction of the femur commences. The thigh, crus and pes all participate actively in propulsion. The retraction of the leg is accomplished by several muscles, the most powerful of which lie principally in the base of the tail. Consequently, the tail base is always nearest in position to the leg which is being retracted (Plate I, lower),



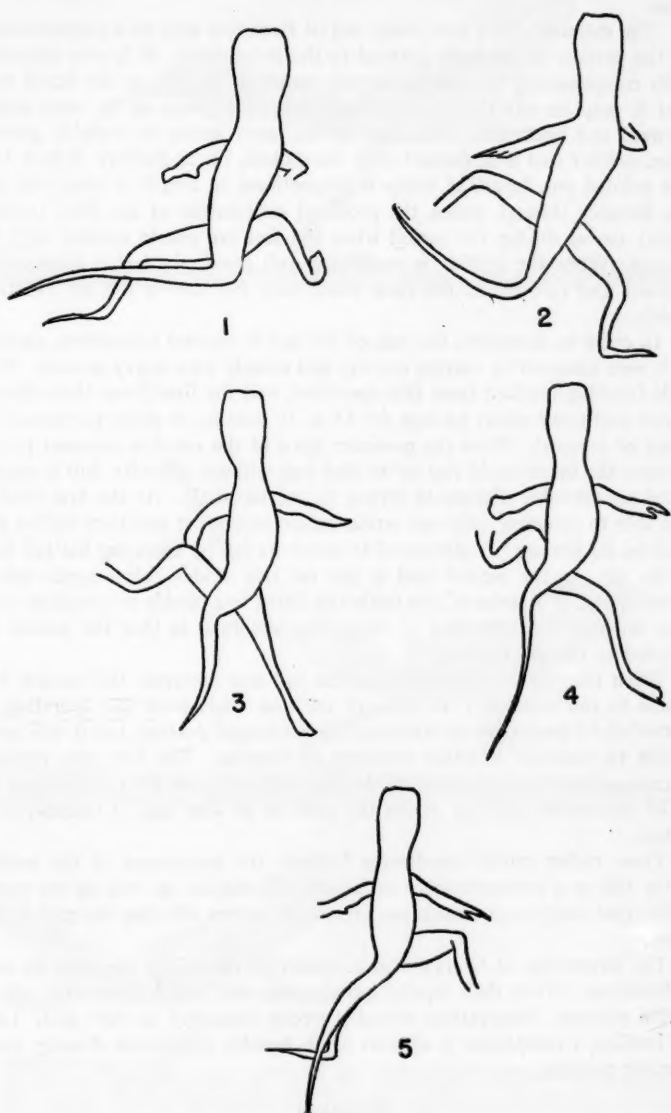


Fig. 2. Posterior aspect of immature *Basiliscus* running bipedally. Locomotor cycle in sequence 1-5. See text for discussion. Made from motion picture by projection.

even though the remainder of the tail may be swinging in the opposite direction.

The extremely long and heavy tail of *Basiliscus* acts as a counterbalance to the portion of the body cranial to the acetabulum. It is also concerned with compensating for changes in the center of gravity as the lizard runs, and it may be effective in providing forward impetus as its mass swings forward and backward. The effect of the latter action is probably greatest when neither foot is in contact with the ground, for as Barclay (1946: 189) has pointed out, length of stride is proportional to length of hind limb and the distance through which the proximal articulation of the limb (acetabulum) moves during the period when the feet are not in contact with the ground. When the basilisk is running at full speed, the tail is often swung upward and forward at the time when both feet are in the air (Plate I, middle).

In order to determine the role of the tail in bipedal locomotion, sections of it were removed by cutting quickly and cleanly with heavy scissors. Very little bleeding resulted from this operation, and the lizard was then allowed to rest and move about its cage for 15 to 30 minutes in order to obviate the shock of removal. When the posterior third of the tail was removed in this manner, the lizard could rise to its hind legs without difficulty, but it experienced considerable distress in trying to run bipedally. At the first trial, it was able to complete only one stride before staggering and then falling forward on its forelegs. It attempted to arrest its fall by elevating the tail high in the air. In the second trial it ran for two strides before again falling forward, and in a series of five trials the lizard was unable to complete more than three strides, the third of which was abnormal in that the animal attempted to shorten the step.

When the posterior two-thirds of the tail was removed, the basilisk was unable to run bipedally. In three of the four trials after this operation, it succeeded for an instant in attaining the two-legged posture, but it was quite unable to maintain it either standing or running. The first step resulted in unco-ordinated movements of the legs and tail, and after continuing its initial momentum halfway across the tank on all four legs, it floundered to a stop.

These rather crude experiments indicate the importance of the weight of the tail as a counterbalance in bipedal locomotion, as well as the probability that length and motion are important factors affecting the gait of the lizard.

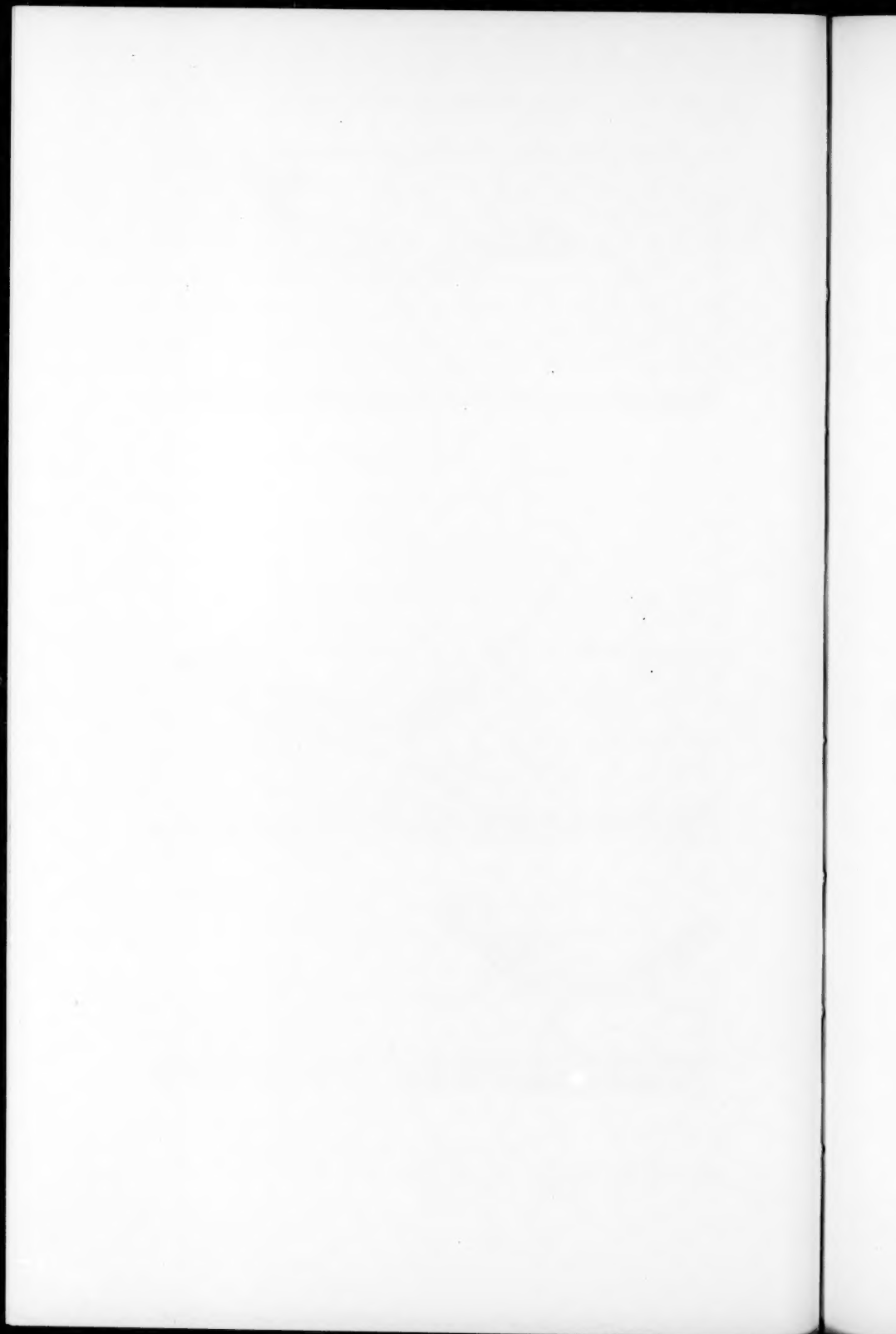
The locomotion of *Crotaphytus c. collaris* is essentially the same as that of *Basiliscus*. While their bipedal running was not analysed with the aid of motion pictures, observations reveal a strong similarity in their gait. Like the basilisk, *Crotaphytus* is able to begin bipedal locomotion directly from a resting position.

#### SUMMARY

1. The iguanid, agamid and teiid lizards, reputed by various authors to have a bipedal or partially bipedal gait, are listed.
2. The bipedal gait of *Basiliscus basiliscus* is described and the major



Upper: beginning of the bipedal gait. The left hind leg is moving forward as the right completes its propulsive stroke. Center: the lizard is running at full speed and the tail is swung upward and forward while both hind feet are off the ground. Lower: the legs are widespread and the tail base is closest to the left leg, which is being retracted. See text for further discussion. (Strobilite photographs by Dr. A. A. Allen.)



differences between it and the gait of other bipedal animals are indicated.

3. The role of the forelegs, hind legs and tail in initiating and maintaining bipedal locomotion is discussed.

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Records of *Macrochelys temminckii* in Oklahoma<sup>1</sup>

By BRYAN P. GLASS

SCIENTIFIC journals seem to contain only two records of the alligator snapping turtle from Oklahoma. A 50-lb. specimen (1)<sup>2</sup> recorded by Wickham (1922) was captured in September, 1915, from the Washita River at Aylesworth Ferry, a locality now beneath Texoma Lake. This turtle was later tagged and liberated in the Blue River northeast of Durant. Pope (1939) referred to this specimen in his remarks concerning movements of these animals. The other record (2), based on a carapace in the Mountain Fork River 14 miles southeast of Broken Bow, McCurtain County, is by Trowbridge (1937). Neither Ortenburger nor Force record *Macrochelys* as occurring in the parts of the state covered by their studies. There are no Oklahoma specimens in any of the larger American museums, nor even in the University of Oklahoma Museum of Zoology.<sup>3</sup> Correspondence with the various colleges and universities in the eastern half of the state has revealed that none of the five institutions replying possess either specimens or records of this species.

It has been a matter of considerable surprise to learn of numerous recent verifiable records for the state. It appears that this turtle is far from rare in eastern Oklahoma. Six records are in the form of anonymous news items in the *Oklahoma Game and Fish News*, a monthly publication of the State Game and Fish Department, each accompanied by a photograph of sufficient clarity to make identification positive. Briefly they are as follows: A 95-lb. specimen (3) captured in November, 1941, along a sandbar in the Kiamichi River near Antlers, Pushmataha County (Anonymous, 1946b). A 70-lb. specimen (4) taken from the Blue River 6 miles north and 14 miles east of Tishomingo, Johnston County, January 2, 1946 (Anon., 1946a). A 100-lb. specimen (5) taken in the summer of 1946 from the Deep Fork River 3 miles south and 1 mile west of Okmulgee, Okmulgee County (Anon., 1946c). An 80-lb. specimen (6) from Sansbois Creek south of Stigler, Haskell County, taken in May, 1947 (Anon., 1947a). A 66-lb. specimen (7) from Rocky Ford on Dirty Creek 6 miles southwest of Keefton on the McIntosh County line, also taken in May, 1947 (Anon., 1947a). A sixth specimen (8) weighing 58 lbs. was photographed while on display at the Muskogee State Fair in October, 1947 (Anon., 1947b). Inquiry reveals that the turtle came from Greenleaf Lake, an artificial impoundment in Muskogee County. The local people are familiar with this form, which they call "loggerhead" and it is considered numerous in this lake and all surrounding waters (Purdy, *in litt.*).

Another record (9) rests on a photograph and news item in the newspaper *The Tulsa World* on July 1, 1947. The turtle, weighing 104 lbs, had been taken in the net of a commercial fisherman in a small lake south of

<sup>1</sup> Contribution No. 142, Oklahoma A and M College, Department of Zoology.

<sup>2</sup> Numbers in parentheses correspond to numbered localities on the map.

<sup>3</sup> Since this article was submitted for publication a 21 lb. specimen taken June 15, 1948, from the Kiamichi River, 3 miles southwest of Clayton, Pushmataha County, has been added to this collection.



Ponca City, Kay County. The exact location of this lake remains uncertain, but the whole area is in the Arkansas River drainage. It seems logical that the turtle might have been trapped behind the impoundment while living as a young animal in the small stream. Still another record (10) is repre-

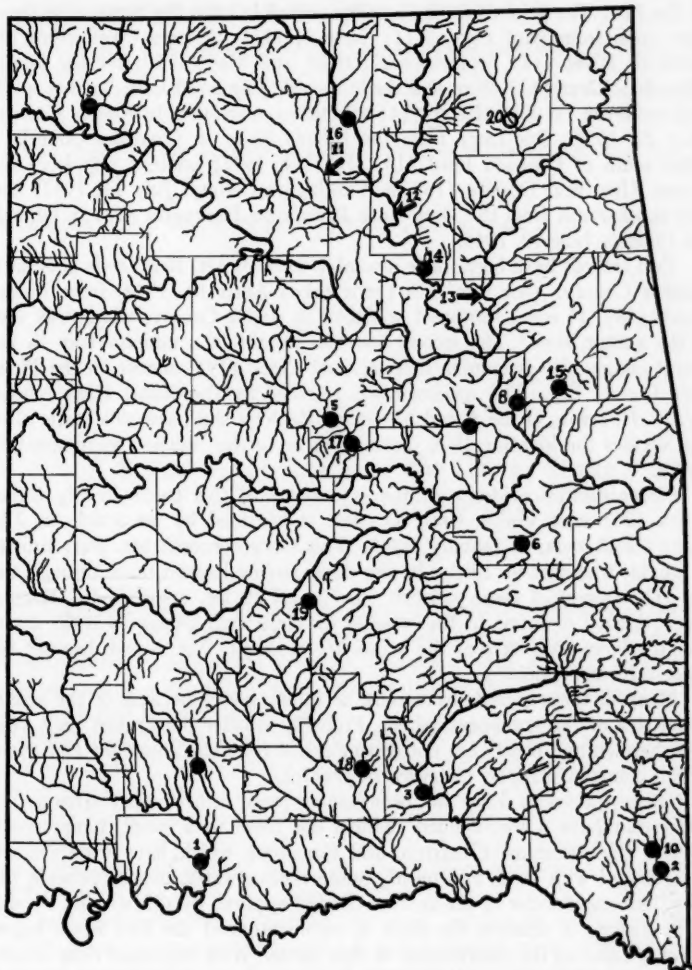


Fig. 1. Distribution of the alligator snapper in eastern Oklahoma. Solid dots mark locations from which specimens have been positively identified. Hollow dots mark probable but unverifiable records. Arrows indicate rivers from which records are verifiable but for which more exact locality data are lacking. For explanation of numbers see footnote No. 2.

sented by a carapace<sup>4</sup> from the Mountain Fork River. The turtle was taken by fishermen near the bridge where U. S. Highway 70 crosses this river, during May, 1947. Judging by its size this turtle probably weighed approximately 35 lbs.

At the Tulsa Zoo, Director Hugh S. Davis has been the recipient of 8 specimens since the year 1930. Dates quoted below are the dates of receipt at the Zoo. For 4 of these the locality record is only the name of a river. One came from Bird Creek (11) June 3, 1931; 2 were taken from the Verdigris River (12) September 27, 1930, and May, 1940; for the Grand (Neosho) River (13) there is a single record, July 31, 1930. A third specimen from the Verdigris River (14) was taken near Inola in Rogers County, May 29, 1939. One came from the Illinois River in Cherokee County, 2 miles south of Cookson Ford (15), July 14, 1941; another was from the Caney River near Ocelata (16) in Washington County, July 11, 1942; and still another was from the Deep Fork River near Henryetta (17) in Okmulgee County, June 19, 1946.

Two records have been made available through Mr. Ben Lewis of Stuart, Hughes County. One was of a turtle taken April 10, 1948, from Magee Creek (18), 15 miles southeast of Atoka in Atoka County, which was sent to the author alive.<sup>5</sup> The second one was caught in a minnow trap in the Stuart community swimming hole on Coal Creek (19), almost on the Pittsburg County line. The specimen was retained by the Stuart High School. Dr. W. H. Irwin, of the A and M College Zoology staff, saw this turtle alive and verifies the identification. Both of these turtles weighed approximately 30 lbs.

Circumstantial evidence of the occurrence of this turtle in Big Cabin Creek (20) near Vinita, Craig County, is provided by an article in *The Daily Oklahoman*, in January, 1948. This story concerns Mr. Burl Brown, of Vinita, who shot 96 turtles in two days, having located them through the ice. The largest of these weighed 60, 70 and 80 lbs. respectively. Even a precautionary discount in the weights of these animals leaves little doubt that the large ones were of the genus *Macrochelys*. Mr. Brown has not replied to further inquiries.

Many of these records have come to public notice because of the sensational size of the specimens taken. Probably smaller ones taken each year by fishermen and others are not distinguished from the abundant and widespread common snapper, *Chelydra serpentina*.

These specimens have all been taken from rather small streams, or rivers that have a well-defined channel not filled with sand. Large rivers such as the Arkansas, Cimarron, and Canadian, which have wide shallow beds choked with sand, and mostly subterranean water, do not provide the deep permanent water or the amount of food required by this species. It will be interesting to observe the effect of stabilization of the Red River below Texoma Lake on the distribution of this turtle. With improved river conditions it should become established in the main stream. Similar results may be expected when projected impoundments on other large streams are completed.

<sup>4</sup> Oklahoma A and M College, Museum of Zoology, No. T-115.

<sup>5</sup> Oklahoma A and M College, Museum of Zoology, No. T-116.

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## A Sexual Aggregation of the Garter Snake *Thamnophis butleri* (Cope)

By L. C. FINNERAN<sup>1</sup>

THERE is a dearth of information on sexual behavior of snakes. One has only to review the literature to note the lack of details and the abundance of generalities. The present paper is concerned with a single afternoon's observations on a small, interlocked aggregation of snakes, apparently of the type popularly termed "snake balls."

These observations were made on April 19, 1948, at 3 P.M. A warm wind was blowing. The sun had shone steadily for approximately four hours, but, at this time, the sky was beginning to cloud over and the sun disappeared intermittently for short periods. The air temperature was 81° F. and a thermometer lying on the ground one foot from the group of snakes during the entire observation read 88°. The site of these observations is an open field lying off the northeast corner of East Jefferson and Ten Mile Road, St. Clair Shores, Michigan. This field is small, rectangular and covered with a thick growth of weeds and grasses. It is surrounded on three sides by well traveled roads and on the fourth by a canal draining into Lake St. Clair. A commercial structure occupies the southern section of the field.

<sup>1</sup>I wish to express my appreciation to the following persons who have read and commented on this paper: Dr. F. A. Beach of Yale University; Dr. E. A. Newcomb of Wayne University; Dr. H. K. Gloyd of the Chicago Academy of Sciences.

## FIELD OBSERVATIONS

An aggregation of six garter snakes (*Thamnophis butleri*) was observed. The snakes were absolutely quiet. The posterior two-thirds of their bodies were extended in parallels. This was noted of four males who covered a particularly large female. The anterior end of the female lay in a coil with the head in the center. The anterior portions of the other snakes were grouped in a ball dorsal and lateral to the coil of the female. A comparably small sixth snake was lying entirely in the ball formation. This animal was not sexed. The chin of one male rested on the female's neck. One of the males was noted to have his cloacal region looped over another male.<sup>2</sup>

Movements were observed twice during a 12-minute period. Lateral muscular contractions in the anterior third of a male were noted for 5 seconds. A second time, the sun disappeared behind a cloud and after approximately 30 seconds, four of the snakes had raised their heads out of the ball. The heads "melted" into the ball when the sun shone again.

After 12 minutes, these observations were interrupted by a movement to the left and extreme rear of the observer's visual field. A seventh snake was seen moving almost in the immediate direction of the grouping. He did not have his snout lowered, as Noble (1937: 70) describes, and was seen to extrude his tongue with every 8 or 12 inches of forward movement. As the animal drew within 3 feet of the others, it made an abrupt 90° turn and proceeded in a semi-circle to the group. The newcomer touched two of the males with his tongue and crossed over them toward the female. He immediately followed the female's body to the tail and doubled back to her neck. Here the male stopped and adjusted his body to that of the female. This behavior evoked marked activity on the part of the other males and the group in general commenced lateral muscular contractions. After 90 seconds, all was quiet. Two minutes later, the comparatively small snake started out of the ball and escaped. Because the group appeared to be disturbed and about to disperse, the entire aggregation was collected. Not one attempted to bite, but the female voided a large amount of yellow material. None of the other cloacal openings were dilated nor was there any visible evidence of copulatory activity.

## FIELD EXPERIMENTS

Before coming on the gathering, three other *T. butleri* had been taken in an adjacent field. They were sexed as a female and two males. The larger male, when released just to one side of the path of the above described seventh snake, remained motionless for 25 seconds and then proceeded to examine the terrain minutely with his tongue. At length he reached the path of the seventh snake and made an abrupt left turn. He followed this path (heading away from the aggregation area) for about 3½ feet and then was picked up. While trailing, he moved his head from side to side and continually extruded his tongue. This snake was then placed on the trail headed toward the group area. He was observed to make a right angle turn just as

<sup>2</sup> Pertinent to this observation are unpublished laboratory experiments dealing with mating preferences of a sexually active male. If while courting a female, the cloacal loop of the male is placed on another female, he will continue with no readjustment as long as the two females stay within reasonable proximity. He will also continue without readjustment if his cloacal loop is placed on another male, although the new male will move out of range immediately, causing the courting male to readjust on the female.

the other male had done and to semi-circle into the area where the congregation had been. There he made two complete circles and then escaped.

The previously-captured female was released on the same spot as the male. She remained stationary for about 4 seconds and then crawled directly across the path that the male had just followed. Her movements were slow, but she showed no behavior like that of the male.

The third snake was set down in the same place as the other two. He paused for about 15 seconds, made a lingual examination of the ground and started off; but instead of making an abrupt turn, this animal followed the track of the released female. Only then was it realized that he had been put down on her path and was probably trailing her. He headed away from the observer and it could not be seen whether this snake was using his tongue, but his head could be seen moving from side to side.

#### DESCRIPTION OF GROUP

The male that arrived last measured 546 mm., tail 130 mm. The measurements of the rest of the group are as follows:

	Total (in mm.)	Tail (in mm.)
Female	572	117
Male	440	65 (part missing)
Male	467	105
Male	525	130
Male	565	137

Dissection showed the largest specimen to be a "ripe"<sup>3</sup> female bearing twenty-four ova averaging 13 mm. in length.

#### REVIEW OF LITERATURE

Situations similar to that recorded above have been noted by Ruthven (1912: 19) who reported five snakes (*T. butleri*) competing for one female and by Breder who stated that "five snakes [*T. sirtalis*] were found in a tangled group. The males making desultory attempts at copulation." Brennan (1924: 52) observed two male garter snakes on the back of a "very large female" and believed them to be copulating. However the ease with which the males broke away would indicate that copulation had not been achieved (see Noble, 1937: 716). A seemingly authentic case of simultaneous copulation among common garter snakes (*T. sirtalis*) has been recorded (Blanchard and Blanchard, 1940). During their observations on mating of the garter snake, the Blanchards noted that: "Sometimes the male shows enough interest to take up position along the female, but does little more, merely lying in the sunshine."

Several authors have also reported trailing behavior. Males of *T. sirtalis* have been observed (Bishop, 1927) to follow the track of a female into the low branch of a hemlock where she was stretched. Davis (1936: 278 and 280) gives evidence of a male *T. radix* trailing a female. Laboratory experi-

<sup>3</sup> The term is Rahn's. Cf. COPELAND, 1942: 233-240.

ments (Noble, 1937) have shown that *T. butleri* will follow a trail made by rubbing body integument on glass plates. The experimenter further reports: "In May, I did not succeed in inducing male *Thamnophis* to follow male trails on glass plate nor females to follow male trails. However, at the end of November, I found *T. sirtalis* which had been in the laboratory several weeks would follow for short distances the trail of one of its own species regardless of sex." Truitt (1927) found a female being followed by males and placed her in "an open-wire fish bucket." This bucket was set at two different times in separate areas. Each time, males were reported to have been found in the vicinity. This observation would indicate that a general olfactory stimulus was operating to bring about a meeting. However, Noble (1937: 701) found that female *T. butleri* and *T. sirtalis*, when placed in bags, or finger bowls covered with perforated paper, did not attract males. Breder (1946: 238) recorded breeding habits of *T. sirtalis* in an aquatic environment. The females lay along the edge of the water and males were noted to be swimming along the edge water frequently stopping to examine lingually the shore line. He notes that "they seemed to be aware of the general area in which the female was located," but that touch was necessary before positive identity was made.

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- 2124 MARLBOROUGH, DETROIT 15, MICHIGAN.



## Herpetological Notes

**NOTES ON NEW-BORN GABOON VIPERS.**—A 4-foot Gaboon viper (*Bitis gabonica*) arrived at the Chicago Zoological Park on May 19, 1948, in fine condition. As in all *Bitis* specimens, disturbance in shipment had a tendency to produce an emphysematous condition, in which the reptile takes only short breaths till calmed. When deflated to normal the next day, the specimen was seen to be gravid. On June 4, she ate a dove.

On June 28, a total of 27 young were born including one stillborn, one with deformed spine, and 25 perfect replicas of the parent. Of the latter, one was lost through drowning in the deep water of the cage tank. Six were already born before parturition was noticed by the night keeper at 6:45 A.M. By 8 A.M. 19 were born. The others were produced 2 in succession half an hour apart. By 11 A.M. the final count seemed to have been reached, but at 1:40 P.M. another was born. Each remained in the egg membrane for approximately 30 seconds before rupturing it. Within 2 minutes or before the young had opportunity to dry, shedding of the skin was performed with no difficulty. The average length of these specimens was 290 mm., diameter at midbody 16 mm., head 30 mm. long and 20 mm. wide, tail 20 mm., fangs 8 mm. The split horn of the adult was not present but a hard split scale is evident. The young snakes were not as pugnacious as the adult and looped off in sidewinder fashion when being transferred to a cage of their own.

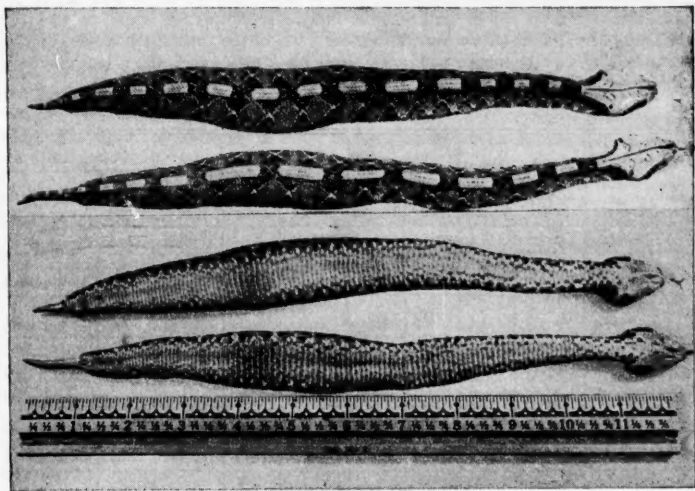


Fig. 1. Baby Gaboon vipers; ♀ above, ♂ below.

On the eighth day, feeding was begun. Seven mice about 2 weeks old were offered and immediately accepted. The babies made no preliminary investigation of the prey but on seeing movement attacked. The food animal was not released by the snake but held in the mouth and juggled into a swallowing position. Later in the day, 14 new born rats were offered and taken. Four specimens ate 2 after the 8 non-feeders had refused them. The deformed specimen was among the latter. In one instance, 2 of the babies fought vigorously over a mouse—the aggressor had previously had his meal—and had to be separated.

When disturbed, some individuals have been noted to flatten the body so markedly into the gravel of the cage bottom as to appear at least three times the normal width. Similar flattening is seen in the late afternoon in a patch of sunlight which enters the cage at that time of day.

Presumably this is the first litter of this species to be born in the United States as a check of the available literature by Mr. Dwight D. Davis of the Chicago Natural History Museum revealed no previous records.—ROBERT SNEDIGAR and EMIL J. ROKOSKY, *Chicago Zoological Park, Brookfield, Illinois.*

**THE BLACK-HEADED SNAKE IN SOUTHERN INDIANA.**—In a recent paper (Minton, S. A., 1944: Amer. Midl. Nat., 32: 472-473), I reported the crowned snake, *Tantilla coronata coronata* Baird and Girard, from the vicinity of New Albany, Indiana, on the basis of two specimens, both of which had been lost. Since then, four additional specimens have been collected near New Albany, confirming the state record and marking a range extension of about 85 miles to the northeast. Two of these specimens are in the writer's collection; one was presented to the University of Michigan Museum of Zoology, and one to the University of Louisville.

I have examined the specimens of *Tantilla c. coronata* in the University of Michigan Museum of Zoology and the data sheets compiled by Blanchard (1938, Zool. Ser. Field Mus. Nat. Hist., 20: 369-376) in his study of the genus for comparison with the Indiana specimens. The characters showing considerable variation (ventral and caudal counts, body length, tail length, and width of the black neck-band) are tabulated. Dorsal scutellation shows no variation. The head shields are remarkably constant in number and arrangement, showing few deviations, none of which are correlated with sex or geographic distribution. It will be seen that the Indiana specimens fall within or very close to the limits of variation of the species in other parts of the country; however, they are characterized by slightly smaller size, a narrower black neck-band, and a low number of subcaudals in both sexes.

	No. of Specimens	Locality	Ventrals		Caudals		Width dark neck-band in scale rows		Length (mm.)			
			Range	Average	Range	Average	Range	Average	Body		Tail	
									Range	Average	Range	Average
M A L E S	3	Indiana	136-141	138.6	42-44	43.3	2-2½	2+	130-182	148.6	35-42	37.6
	5	Ky. and Tenn.	134-138	135.0	42-48	45.3	3-4	3½	183-210	192.6	44-48	46.0
	19	Gulf Coast	131-137	134.4	41-50	47.0	2½-5	4	76-199	148.7	21-48	38.3
	18	Eastern Coastal Plain	131-141	135.2	42-51	47.3	1-5	4+	86-211	163.9	23-52	42.2
F E M A L E S	1	Indiana		143		36		2		150		35
	6	Ky. and Tenn.	140-148	143.5	39-46	43.0	1½-3	2+	176-264	212.0	39-60	46.0
	14	Gulf Coast	139-147	141.7	40-50	44.9	3½-4½	4+	80-218	150.2	18-44	33.4
	11	Eastern Coastal Plain	140-147	144.1	37-46	43.5	3-4½	4+	102-222	181.9	23-50	39.5

These snakes were collected along the crest of the Knobstone Escarpment from Renn's Spring about 5 miles north of New Albany to Barrel Chute Knob on the Floyd-Clark county line west of St. Joseph. Their habitat seems restricted to the immediate vicinity of the bare claystone slopes, which give this area the local name of Bald Knobs. With the exception of one individual coiled in the sun at the base of a sandstone ledge, all specimens were found under logs or stones. They are found in drier situations than

are *Carphophis* and *Diadophis*, the other small snakes of the area. In Floyd County, *Tantilla* seems to be associated with *Cnemidophorus sexlineatus* quite consistently. It has been found in all but two of the known *Cnemidophorus* colonies and *Cnemidophorus* has been collected at all sites where *Tantilla* has been found. This association seems to be based on the preference of both reptiles for a dry habitat. *Tantilla* has been collected as early as March 29 and as late as October 16. Three of the specimens were secured following periods of heavy rain.

Microscopic examination of feces voided by one specimen shortly after capture showed segmented chitinous material apparently of arthropod origin. It seems likely that insects and centipedes comprise the bulk of their diet.

A specimen collected May 30 showed two or three elongated eggs visible through the semi-translucent ventral plates. Unfortunately, this snake escaped before the eggs were laid.

Two specimens kept in a terrarium lined with a mixture of sand and loose soil persistently avoided the slightly moist area around their drinking pan. They were always found concealed during the day, but several times were seen actively prowling on the surface after dark. A variety of centipedes, insect larvae, and worms were offered as food. Some of these disappeared, but the snakes were not observed feeding.

Although classified among the rear-fanged snakes, it is doubtful if *Tantilla* is venomous even to the small creatures upon which it feeds. Perkins (1938, Bull. Zool. Soc. San Diego, 13: 47) failed to find poison glands in microscopic sections of the heads of the western species, *T. ciseni*. I forcibly induced a specimen to bite an earthworm, which did not show any ill effects.

It is impossible to state at present whether the black headed snakes taken near New Albany are from an isolated population or whether the species is more or less continuously distributed through southern Indiana and adjacent portions of Kentucky and Illinois. It has a continuous range through the austroriparian region to western Tennessee and southwestern Kentucky. Hibbard, (1936, Trans. Kansas Acad. Sci., 39: 281) reports it as common in the Mammoth Cave area of Kentucky, and Taylor (1936, ibid, 39: 335) lists two specimens from Cedar Springs Valley, Edmonson County, Kentucky, some 80 miles southwest of New Albany. There are no records for southern Illinois in spite of considerable herpetological collecting in this area. Since the Norman Upland, of which the Knobstone Escarpment is a part, is continued south of Louisville as the Muldraugh Hills, this would seem a likely region to seek further specimens of this snake.

In conclusion, I wish to extend my thanks to Dr. Howard K. Gloyd and Dr. Frieda Cobb Blanchard through whose courtesy I was permitted to examine unpublished data compiled by the late Dr. Frank N. Blanchard. I also wish to thank Dr. Norman Hartweg of the University of Michigan Museum of Zoology for his advice and criticism. I am most grateful to Messrs. Frank Powell, John Minton, and Harry Carnighan for their invaluable assistance in the field.—SHERMAN A. MINTON, JR., *Indiana University Medical Center, Indianapolis, Indiana.*

NOTES ON THE FOOD OF THE INDIGO SNAKE.—While examining for parasites a 6-foot indigo snake, *Drymarchon corais couperi* Holbrook, captured November 7, 1948, 8 miles west of Royal Palm State Park, Everglades National Park, on route 207, two snakes identified as *Sistrurus miliarius barbouri* Gloyd and four turtle eggs were discovered in the digestive tract. The ground-rattlers, measuring 12 and 14 inches, had been engulfed head first and were found head to tail in the esophagus. Of the four elliptical turtle eggs, whose average measurements were  $1\frac{1}{4}$  inches by  $\frac{1}{2}$  inch, two were in the esophagus and two in the small intestine shortly posterior to the pyloric stomach. Egg-shell fragments, as well as gravel and small stones, were scattered throughout the length of the intestines.—WILLIAM A. BABIS, *University of Miami, Coral Gables, Florida.*

## Ichthyological Notes

FIELD NOTES ON THE MINNOW, *GILA DITAENIA*, IN SOUTHERN ARIZONA.—During early October of 1944, in company with Dr. A. J. van Rossem, I made my first visit to Sycamore Canyon (=Bear Canyon) of the Pajarito Mountains, Santa Cruz County, Arizona. This picturesque gorge drains southward across the Mexican boundary into the desert of Sonora, so we looked upon it as a potential highway for the northward diffusion of Mexican species of birds into United States territory. Why should it not serve equally well for the movement of other organic species, developed then as a natural question. I was, therefore, immediately interested when I discovered tiny fish in some shallow pools beside our camp, and considerable effort was expended in collecting a small number of them. These specimens were sent to Dr. Carl Hubbs who informed me that they represented a new species which was at that time being studied by Dr. Robert R. Miller, from specimens obtained in the Río Magdalena of Sonora, Mexico. Dr. Miller's study appeared the following spring, designating the species as *Gila ditaenia* (COPEIA, 1945: 104-110).

During the succeeding two years, we made repeated visits to Sycamore Canyon for ornithological work but the little fishes continued to interest me, with the result that several items concerning them were accumulated. These notes are herewith offered to ichthyologists because but few scientists seem to have met the species in its native waters.

Our camp was always located at a spot called Yank's Spring near the crumbling walls of an old adobe ranch house that had been raided and burned by the Apaches more than 50 years before. More recently the spring itself has been cleared out and its waters led to a concrete cattle tank some 50 or 60 yards up the side slope from the bed of the canyon. This sizeable tank has been stocked with minnows from the stream bed pools and the fish have done well there, resulting in a large population, including some specimens of maximum size. These fish have no way of reaching the small pools in the stream bed. Slightly more than half a mile down the dry canyon, water is again forced to the surface by bedrock and here there is a natural pool about three feet deep and ten feet long that contains adult fish. Water trickles into this pool over a nearly vertical rock face about two feet high but with irregularities enough to serve as a rather difficult fish ladder. After a brief shower one summer, a very trout-like activity of *ditaenia* was noticed at this basin. The spot had been visited at least twice daily during each of our many previous trips to Sycamore Canyon without my having seen any special restlessness of the fish. After the shower, however, the fish were greatly stimulated. Even before reaching a point where the water became visible beneath a cut bank, I noticed a distinct sound which came from the leaping and splashing of the tiny fish. They were climbing the natural fish ladder up the face of the rock. Every third or fourth attempt carried a frantically wriggling little fish up and over the crest to some shallow pools above.

The thirsty soil of the canyon slopes had absorbed the storm water about as fast as it fell and no perceptible run-off seemed to have reached the pool. Certainly there was no current established through it since its main body lay to one side of the intake and the coarse sand bar at its lower limit was still "high and dry." The upstream urge that led to active jumping by dozens of little fish must have been derived from some biochemical stimulus. A measure of stagnation in the pool had been suspected on various visits because there was always a crowding of the smaller specimens into a dense school at the foot of the intake trickle. After the shower there was no increased current in the stream that was perceptible to me though it must be conceded that an anadromous fish would be far more sensitive and ready to react to rheotrophism than a human being. My own suspicion is, however, that the hydrogen-ion concentration had been changed and that a chemotropic response was being observed in this case.

The first specimens submitted to the ichthyologists were very small ones which were furthermore captured with some difficulty by using raccoon methods. Ornithologists generally consider a can-opener as the ultimate in fishing gear that will be called for in the semi-desert of southern Arizona. The shallow waters contained no large sized fish

but several charges of bird shot finally brought to hand a medium sized specimen that displayed enough added characters to stimulate the desire for a really mature individual. One day as I sat resting by the large pool, a small yellow leaf fluttered down to the surface and was immediately "struck" by a fish that rose from its deep-water hiding-place as a trout would rise to a fly. Like the small fish, I also was activated by a "release mechanism" which turned my clock back fully sixty years and I sped up the canyon to our camp. One of my all too few pins was bent into a hook, strung on coarse sewing thread and weighted with a split buckshot. With a willow pole and the pectoral muscle of an Arizona whippoor-will as bait, my barefoot boy equipment was complete. With it a goodly series of "whoppers" were brought up from the depths where they had remained in hiding heretofore. No attempt was made to play the fish since the pin hook had no barbs on it and a good many fish flopped off the hook before being landed. Still, the biggest one did *not* get away.

The adult fish are handsome little fellows with carmine-rose areas along the sides and belly, interspersed with shining dark green. Unfortunately more careful color notes were not recorded and my Kodachrome exposures were not well lighted.

There is no permanent water in Sycamore Canyon above our camp site at Yank's Spring and I have not explored downstream beyond the international boundary, approximately five miles distant, but it has no water-bearing tributaries within our territory. One small colony is therefore all that we have to represent this little known native species. Yank's Spring lies at an altitude of approximately 4000 feet and the canyon drops down rather steeply out of the Pajarito Mountains to semi-desert country as we saw it from a nearby overlook. I imagine, therefore, that only rarely if ever does a rainy cycle provide a water way for the fish to contact their fellows of the Magdalena River in Sonora.

For the benefit of all students of the geographic distribution of fresh-water fishes, I wish here to report that, during one of our visits to Sycamore Canyon, a group of men drove up in a truck with live containers to seine fish from the concrete tank. I told them that the fish represented an undescribed species and asked them to report any transplantings to state and federal authorities. I could learn nothing of their plans and my suggestions brought forth no response. I had therefore no recourse but to respect their right to silence (with a minimum of respect) and hope that no ichthyologist of the future would be disturbed by finding specimens of *Gila ditaenia* in waters where it had no right to be living.

The nearest large canyon to the eastward in the Pajarito Mountains is Peña Blanca Canyon, which heads in a spring only five miles by airline from Yank's Spring. I had heard reports some years previously that there were minnows in this latter spring but I have never been able to determine the truth of that report.<sup>1</sup> About the same distance to the westward, Arivaca Creek arises but I was told that artificial plantings in its only permanent water—a sizable tule pond—had been made. At my latest visit no fish of any sort in this pond were known to any of the people of the area whom I could contact.

Both Peña Blanca and Arivaca Creeks flow northward, however, and eventually drain into the Santa Cruz, Gila, and Colorado rivers, reaching the Gulf in Mexican territory. In the Colorado-Gila River system there occurs a larger congener of my little fish, *Gila robusta elegans*, locally called Gila trout or bonytail, but at this point in geologic history the two sister species are isolated in two fresh-water systems that approach each other within five miles at their headwaters but with their mouths separated by nearly 300 miles of salt water in the Gulf of California. The long trough of the Gulf with its transverse sill extending westward from Tiburón Island is seemingly the result of a down dropping fault block. Both the Gila-Colorado and the Magdalena-Altar systems drain into the Gulf basin that lies north of the Tiburón sill, a basin that might very properly have been a fresh-water lake at a time not too remote in the geologic past. Such times may also have seen less desert conditions in southern Arizona and northern Sonora. Peña Blanca Canyon and Sycamore Canyon may then have been occupied by lusty, living streams that flowed respectively into Santa Cruz and Altar rivers, which were not rivers of parching sands as they are today throughout most of the year,—rivers

<sup>1</sup> Since this note went to press Mr. Gilbert Sykes of the U.S. Forest Service has verified for me the presence of fish in A'lamo Spring at the head of Peña Blanca Canyon.

that were united into one great fresh-water system by way of a lake north of the Tiburón sill,—rivers that were quite hospitable to the ancestors of both the Gila trout and my colorful little fish of Sycamore Canyon.—LOYE MILLER, *University of California, Los Angeles, California.*

A RECORD OF LUTJANID FISH (*LUTJANUS CYANOPTERUS*) FOR THE ATLANTIC COAST OF THE UNITED STATES, WITH NOTE ON RELATED SPECIES OF THE GENUS.<sup>1</sup>—Among the Western Atlantic representatives of the family Lutjanidae (snappers) are included four closely related species which form a compact and well defined group within the genus *Lutjanus*. These are: *L. cyanopterus* (Cuvier and Valenciennes, Hist. Nat. Poiss. 2, 1828: 357, Brazil), commonly known in the West Indies (Cuba) as "Cubera"; *L. griseus* (Linnaeus, Syst. Nat., ed. 10, 1758: 283, after Catesby, Bahamas), the well known gray or mangrove snapper; *L. jocu* (Bloch and Schneider, Syst. Ichth., 1801: 310, after Parra, Cuba) the dog snapper; and *L. apodus* (Walbaum, Artedi Piscium, 1792: 351, after Catesby, Bahamas) the schoolmaster.

Of the above species, all but *L. cyanopterus* are common in Florida, especially throughout the Keys, but that species has not heretofore been reported from the United States.

Recently, through the courtesy of Albert Pflueger, the well known taxidermist of Miami, Florida, a large specimen of *L. cyanopterus* weighing 80 pounds and measuring 1000 mm. in standard length, was donated to the Marine Laboratory of the University of Miami. This specimen was captured off Fort Pierce, Florida, on May 4, 1948, and it is believed to be the first record of the species for the United States. A brief description of the specimen follows:

Head 2.6 in standard length; depth 2.6. Least depth of caudal peduncle 3.1 in head. Maxillary 2.15 in head, reaching somewhat beyond vertical from anterior margin of orbit. Orbit 8.9 in head, 4.2 in maxillary, 2.1 in interorbital, 3.7 in snout. Interorbital 4.65 in head, 2.15 in maxillary. Snout 2.5 in head, 1.1 in maxillary. Pectoral fin 1.6 in head, its tip reaching beyond tip of pelvic by a distance about equal to twice diameter of orbit. Pelvic fin 2.2 in head, equal to distance between tip of snout and center of eye. Middle caudal rays 2.4 in head. Dorsal X-13½; anal III-8½; pectoral 17; branched caudal rays 15. Scales in 47 transverse rows between "scale bone" and caudal base. Gill rakers 5 on lower limb of first arch, not counting rudiments, which are absent on left arch.

It is now known that large specimens belonging to this species are occasionally taken in south Florida waters, but have been confused hitherto with *L. griseus*. Both species are closely related and look very much alike superficially. Most Florida fishermen call these large specimens of *L. cyanopterus* "overgrown mangrove snappers." However, recent conversations with commercial fishermen experienced in West Indian waters have disclosed the fact that these men are able to distinguish both species and refer to *L. cyanopterus* by the name of "Cuban snapper," because this species is commonly taken in Cuban waters.

*Lutjanus cyanopterus* is one of the largest species of the genus, reaching a weight of 100 pounds or more, but most of the specimens captured usually weigh between 30 and 60 pounds. Small specimens are very rarely taken and practically nothing is known of the habits of this species. *L. jocu* also reaches a large size but small specimens weighing between one and five pounds are usually taken. *L. griseus* and *L. apodus* rarely exceed a weight of 20 pounds and most of the specimens taken weigh less than five pounds.

The following diagnosis and key are intended to serve as a ready means of identification for the species referred to in the present paper.

Fishes of the genus *Lutjanus* with rounded soft dorsal and anal fins and no black blotch on sides of body or base of pectoral fins. Gill rakers 5 to 10 on lower limb of first arch, not counting rudiments. Scales in 39 to 49 transverse rows between "scale bone" and caudal base. Fresh, brackish and shallow coastal waters of the western Atlantic, from Cape Cod to Brazil, including the West Indies.

<sup>1</sup> Contribution No. 29 from the Marine Laboratory, University of Miami.



- 1a.—Vomerine patch of teeth crescent shaped, without a distinct median backward projection. Upper and lower canines very strong, about equally developed. Gill rakers 5 to 7, usually 6 on lower limb of first arch, not counting rudiments. Second anal spine shorter than second dorsal spine, its length more than 2 times in maxillary. Greatest width of head usually less than 1.6 times in distance between posterior tip of maxillary and insertion of pelvic fin. West Indian region including south Florida, and Atlantic coast of Central and South America from Panama to Brazil. *Lutjanus cyanopterus*
- 1b.—Vomerine patch of teeth anchor shaped, with a distinct median backward projection. Upper canines much more developed than the lower. Gill rakers 7 to 10, usually 8 or 9, on lower limb of first arch, not counting rudiments. Second anal spine about equal to, or longer than second dorsal spine, its length less than 2 times in maxillary. Greatest width of head usually more than 1.6 times in distance between posterior tip of maxillary and insertion of pelvic fin.
- 2a.—Pectoral fin about equal to distance between tip of snout and posterior margin of preopercle, 3.7 to 4.2 times in standard length. Greatest depth of body 2.6 to 3.2, usually 2.7 to 3.1 times in standard length. Last dorsal spine 1.1 to 1.7, usually 1.2 to 1.6 times in snout. Second anal spine not reaching to tip of third in young. Atlantic coast of America from Cape Cod to Brazil and West Indian region. *Lutjanus griseus*
- 2b.—Pectoral fin longer than distance between tip of snout and posterior margin of preopercle, 3.0 to 3.5 times in standard length. Greatest depth of body 2.3 to 2.8, usually 2.4 to 2.7 times in standard length. Last dorsal spine 1.6 to 2.2, usually 1.7 to 2.1 times in snout. Second anal spine reaching to, or beyond tip of third in young.
- 3a.—Scales in 45 to 49, usually 46 to 48 transverse rows between "scale bone" and caudal base; 8 to 10 scales between origin of dorsal fin and lateral line, counting downward and backward. A somewhat diffuse whitish bar between eye and area immediately posterior to maxillary. West Indian region including south Florida to Brazil, straying northward to Cape Cod. *Lutjanus jocu*
- 3b.—Scales in 39 to 44, usually 40 to 43 transverse rows between "scale bone" and caudal base; 5 or 6 scales between origin of dorsal fin and lateral line, counting downward and backward. No whitish bar below eye. West Indian region, including Florida to Brazil, sometimes straying northward. *Lutjanus apodus*

In addition to the characters given in the key, one of the best distinguishing features of these species is their distinctive coloration. Unfortunately, the colors are rapidly lost after a short period of preservation and can only be recognized in life or while still in a very fresh condition. *L. cyanopterus* and *L. griseus* have a very similar color pattern consisting of a faint barred effect (vertical) on the sides of the body more conspicuous in young specimens and not evident in older individuals. The dorsal and caudal fins are grayish and the pelvic and anal somewhat reddish. The pectoral fin is almost colorless. The barred effect is also noted in *L. jocu*, and in *L. apodus* the bars are much more conspicuous and persistent, becoming obsolete only in the larger individuals. In *L. jocu*, the dorsal, pectoral and caudal fins are orange-red and the pelvics and anal orange-yellow. In *L. apodus* all the fins are yellow, sometimes with orange hues. The general coloration of *L. cyanopterus* and *L. griseus* is grayish with reddish hues, especially about the head. *L. jocu* is lighter in coloration with a greater proportion of reddish, orange and yellowish hues. In *L. apodus*, the general coloration is decidedly orange-yellow with reddish tinges, especially about the head.

Observations in the field conducted during a number of years, especially in south Florida and Cuba, indicate that these species have broadly overlapping but significantly distinct ecological preferences. Large individuals of *L. cyanopterus* occur along submarine ledges within the continental or insular shelf in water seldom deeper than 10 or 20 fathoms. The same may be said of large individuals of *L. jocu*. As already mentioned elsewhere in this paper, small specimens of *L. cyanopterus* (less than 20 pounds) are extremely rare, a fact which at present I am unable to explain. On the other hand, small and medium sized specimens of *L. jocu* are much more common than large specimens, as would be normally expected. *L. griseus* is by far the most abundant and commonest species, preferring brackish shallow waters (less than 1 fathom) and muddy bottoms, especially in mangrove situations such as "bayous" and tropical estuaries. *L. jocu* and *L. apodus* are also found in this habitat with *L. griseus*, but *L. apodus* seems to prefer more open water and sandy bottom near coral reefs. *L. jocu* does not seem to have very distinct preferences and is apparently at home in all shallow water situations not exposed to continuous intense wave action which the other species also avoid, with the

exception perhaps of *L. apodus*. It is interesting to note that *L. jocu* and *L. apodus* frequently occur in fresh water, sometimes many miles upstream. Breder (Zoologica, 18 (3), 1934: 70) reported *L. griseus* from Lake Forsyth, a body of fresh water in Andros Island, Bahamas, but this species, although common in estuaries, is seldom found in fresh water.

The species referred to above are carnivorous and bottom feeders, preying upon smaller fishes and crustaceans such as shrimp and fiddler crabs. Interesting notes on the feeding and other habits of these species are given by Longley and Hildebrand in their systematic catalogue of the fishes of Tortugas, Florida (Pap. Tortugas Lab., 34, Carnegie Inst. Wash., Publ. 535, 1941: 115-120).

The close relationship and similar geographical distribution of the species discussed herein, as well as their ecology, make one wonder about the possible speciation processes involved in their evolution. They may have evolved "in situ" from a single common ancestor through ecological segregation combined perhaps with a certain amount of geographical isolation; or their ancestors, at least some of them, may be traced to certain East Indian lutjanids through geographical replacement and subsequent total geographical isolation. The general morphology, characters and habits of *L. jocu* suggest a possible hybrid origin for this species, involving *L. griseus* and *L. apodus* as parental species. This, however, is not probable and should be taken as a mere conjecture. These species are not known to hybridize in nature and as far as I know, no attempt has been made to hybridize them in the laboratory. They all remain perfectly distinct and without intergrades in suite of their close relationship and the fact that they occur together.—LUIS RENE RIVAS, Marine Laboratory, University of Miami, Coral Gables, Florida.

**GOLDEYE, *AMPHIODON ALOSOIDES* (RAFINESQUE), OCCURRING IN TWO SMALL STREAMS OF CENTRAL ILLINOIS.**—According to Forbes and Richardson (1920: Fishes of Illinois, Nat. Hist. Surv. Ill., 3: 357) the goldeye is confined to the largest streams in or bordering Illinois, namely: Illinois River, Mississippi River, and Ohio River. Recently we received a request to identify a fish taken by a local sportsman at Lincoln, Illinois. The specimen had been frozen and was in good condition on the date examined, when it was determined to be a goldeye. It is now in the Illinois Natural History Survey collection. The fish was caught on hook-and-line by Mr. William McCann during August, 1948, in Sugar Creek, a small stream in Logan County near Lincoln. Conversations with local sportsmen indicate that several goldeye were caught during the summer and fall of 1948 in Sugar Creek and nearby Kickapoo Creek. Heretofore the goldeye had not been seen by local sportsmen in this area. In early November we seined this creek for two hours but failed to take a single goldeye.

Sugar Creek, varying from 10 to 40 feet in width and from 1 to about 5 feet in depth, is approximately 45 miles long. It is a branch of Salt Creek and a tributary of the Sangamon River, which empties into the Illinois River near Chandlerville. It is about 64 miles from the point on Sugar Creek where our goldeye was caught to the mouth of the Sangamon River. Kickapoo Creek empties into Salt Creek 12 miles above the mouth of Sugar Creek.

No reports concerning the goldeye were received from other parts of the state, and at present we are unable to explain the local occurrence of the goldeye in Logan County streams. The absence of high dams gives fish access to this area from the Illinois River. We have asked several local sportsmen to inform us of future occurrences of the goldeye in anglers' catches.—WILLIAM C. STARRETT and R. WELDON LARIMORE, Illinois Natural History Survey, Urbana, Illinois.

**EMBRYOLOGICAL NOTES ON *MENIDIA*.**—During the summer of 1948, while studying at the Marine Biological Laboratory at Woods Hole, Massachusetts, we found the two common species of *Menidia* in that area, *M. beryllina* and *M. menidia notata*, to be material well suited for embryological work even though the eggs are smaller than those of *Fundulus heteroclitus* and *F. majalis*, the marine teleost eggs most commonly studied at that laboratory. The concentration of the surface threads at one small area of the chorion, the small number of oil droplets, and the extraordinary trans-

parency of the chorion, yolk, and embryo itself give a clearer vision of the internal processes of development. The per cent mortality during transfer from traps to aquaria is somewhat higher for *Menidia* than for *Fundulus*. Once the fish are established in aquaria, however, they survive as well as *Fundulus*, are easily stripped, and the eggs and sperm can be obtained several weeks after the two species of *Fundulus* are apparently spent, i.e., late July.

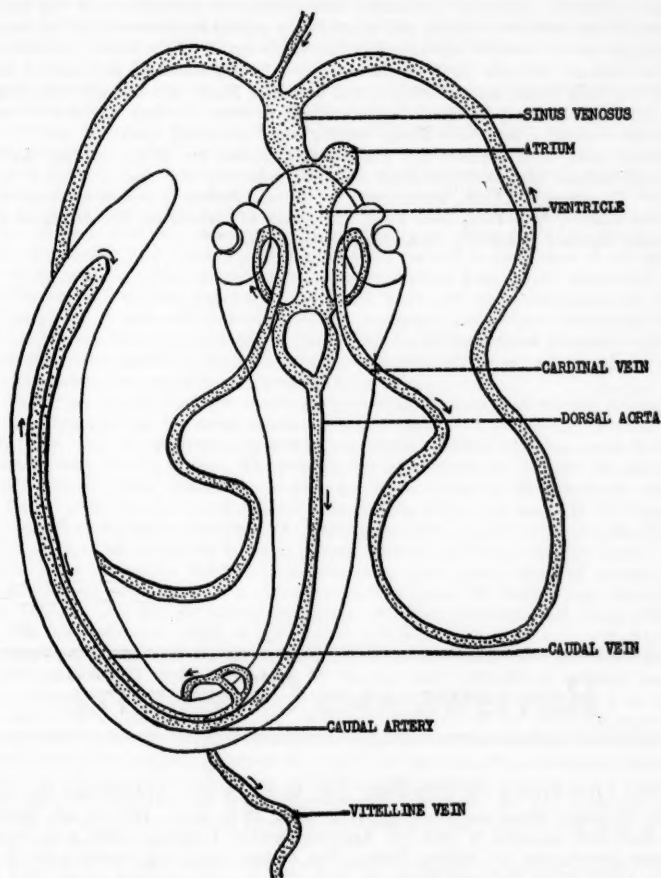


Fig. 1. Circulatory system in a 48-hour embryo of *Menidia menidia notata*.

The embryology of *M. menidia notata* has been studied to some extent by Kunz and Radcliffe (1918, Bull. Bur. Fish., 35: 89-134) and the eggs of *Menidia* species have been described by Ryder (1883, Bull. U.S. Fish Comm., 3: 193-196) and Hildebrand (1923, Bull. Bur. Fish., 38: 113-120). Due to the transparency of the egg, we were able to trace with ease the development of the circulatory system in *M. menidia notata*. The accompanying Figure 1 shows the circulatory system in a 48-hour embryo raised at 24° C.

Moenkhaus (1904, *Amer. J. Anat.*, 3: 29-66) and Pinney (1928, *J. Morph.*, 45: 579-598) have already demonstrated the production of hybrid embryos from crossing *M. menidia notata* with other teleosts. The *M. menidia notata* x *Fundulus heteroclitus* crosses which were reported did not progress beyond the yolk plug stage. Our studies involved crosses of *M. beryllina* with *F. heteroclitus*. Using eggs of *Fundulus* and sperm of *Menidia* we obtained some embryos that survived 14 days (at 23° C). The control pure *Fundulus* embryos started hatching after 12 days. All of our hybrid embryos showed numerous anomalies: a retarded and incomplete development of the nervous system, of the circulatory system, and of somites, a general foreshortening of the body, a smaller size and a "bubbly" appearance of the whole surface of the embryo as compared to the *Fundulus* controls. Most of the embryos exhibited twitching movements; developed eyes with lenses, chromatophores, and a beating heart; and had differentiation of the fore-, middle-, and hind-brain. One embryo survived 13 days and was a nearly shapeless mass of cells with a slowly beating heart projecting from one end. In the reciprocal cross, using *Menidia* eggs and *Fundulus* sperm, the hybrid embryos survived to stages between late embryonic shield and early yolk plug—a period of about 15 hours at 23° C.—EUGENIE CLARK, *Department of Animal Behavior, American Museum of Natural History, New York, New York*, and JAMES M. MOULTON, *The Biological Laboratories, Harvard University, Cambridge, Massachusetts*.

## REVIEWS AND COMMENTS

**THE LIFE STORY OF THE FISH. HIS MORALS AND MANNERS.** By Brian Curtis. Harcourt, Brace and Company, New York, 1949: xii + 284; 1st ed. \$3.75.—This book first appeared in 1938 (D. Appleton-Century Company) with a deservedly generous introduction by William Beebe. The original book was reviewed by R. S. Croker (1948, *Calif. Fish and Game*, 24 (3): 297) in very favorable terms. For the present republication it has been "re-written, with extensive revisions and additions" plus a new chapter.

There seems to be little which might be added to these earlier comments by Beebe and Croker. The present volume is still the same masterpiece of composition, with the story of the structure and habits of fishes, sifted from a voluminous literature, retold in simple words and in a highly interesting way. Even one with a very limited interest in fishes can readily become completely absorbed in the "tale." Humor is an outstanding characteristic of the book. Also the author is clever in presenting simplified interpretations of fish structure in terms of behavior and evolution.—GERALD P. COOPER, *University Museums Annex, Ann Arbor, Michigan*.

FISHES OF THE WESTERN NORTH ATLANTIC. Part One. Lancelets, Cyclostomes, Sharks. Preface (p. xi), by John Tee-Van (unsigned); Introduction (pp. xiii-xvii, 2 maps), by John Tee-Van; Lancelets (pp. 1-28, figs. 1-3), by Henry B. Bigelow and Isabel Pérez Farfante; Cyclostomes (pp. 29-58, figs. 4-5) and Sharks (pp. 59-546, figs. 6-106), by Henry B. Bigelow and William C. Schroeder; Index of Common Names (pp. 547-551) and Index of Scientific Names (pp. 552-576). Mem. Sears Found. Mar. Res., 1, 1948: xvii + 576, 2 maps, 106 figs. \$10.00.—A half century has elapsed since the publication of *The Fishes of North and Middle America* (1896-1900). That monograph, bold in conception and in execution, at once became and has ever since remained the standard ichthyological reference for the continent. It culminated an era of very active research by David Starr Jordan and a corps of associates and students—the “Jordan School” that long dominated the field. Following the flare of activity that accompanied the preparation of that four-volume treatise—a task in which nearly all ichthyologists of the day participated, mostly with only footnote recognition—there ensued a period of stifled progress: the very size and authoritativeness of the monograph led the authors as well as others into the delusion that the ichthyological problems of North America were so thoroughly treated and so nearly solved as to make much more profitable researches on fishes of more distant waters. In time, however, it became evident that the fish faunas of the continent were very incompletely known, that new species and other faunal additions were readily discoverable and that endless gaps existed in knowledge of old species as well as new. The many publications that have resulted have greatly augmented and modified North American ichthyology, rendering more and more antiquated the great monograph by Jordan and Evermann, which, moreover, has become increasingly difficult to acquire; furthermore, it was written solely for ichthyologists. Frequent calls for a new edition, or preferably a replacement, have consequently been voiced, but not until now has a start been made in an answer to those calls.

Unfortunately, but no doubt wisely, the geographical coverage of the new monograph has been restricted to the most completely known sector of the North American fish fauna: the time for continental as well as for global revisions of fishes seems to have passed, at least for the present. The treatise now so auspiciously initiated will comprise a long series of critical revisions by various specialists, embracing all littoral and pelagic fish faunas of the western North Atlantic from Hudson Bay to the mouth of the Amazon, with partial or occasional treatment of related extralimital and adjacent deep-sea forms. May it serve as an inspiration for other general treatises on North American fishes! The marine fauna of western North America stands in much greater need of revision and the fresh-water faunas remain a seemingly endless source of totally new discoveries. Time is hardly ripe for any general monograph of North American fresh-water fishes.

The first volume of *Fishes of the Western North Atlantic* sets a very high standard—perhaps so high a standard as to render difficult the completion of subsequent volumes by authors less well equipped than Henry Bigelow and associates in courage, energy, time, meticulousness, thoroughness, experience, library facilities and willingness to sacrifice much else for this one grand task. The stupendous amount of work that went into this volume is difficult to appreciate by one who has not, for example, attempted the compilation of the complete literature on a species in the form of an organized, annotated synonymy (the synonymy of *Squalus acanthias* alone analyzes more than 350 literature references). Nor is it easy to realize the amount of time, thought and labor that went into the well-balanced summary, for each species, of published and original data on taxonomy and natural history.

In each of the three chapters there is a very informative though rather brief general discussion of the group, with characterization of the larger subgroups and keys down to all families. Families in turn are described, with keys to all known genera. The keys to species within genera often include extralimital forms (with indication of range). Such broadened treatment will not only render easier the identification of additions to the fauna but will also increase the usefulness of the monograph to students of other faunas. It will surely become one of the most used of ichthyological treatises.

The keys are of the dichotomous, outline type, with comparisons restricted to one or a very few characters, and are stated in rather general terms. Such practice will please most users, both lay and scientific, though some critical ichthyologists would welcome more extended comparisons and more precise statements.

The natural order is maintained for genera and higher groups, but within each genus the species are alphabetically arranged. This reversal of standard practice may be excusable on the grounds of convenience, though page references in the index and in keys and, if needed, in an initial alphabetical list for each large genus would seem adequate. Disadvantages are the wide separation of the accounts of closely related species that need frequent comparison and the failure to indicate clearly the interspecific relationships. I hope this policy is not fixed.

For each species the available data are well organized under the following headings: Study Material (generally rather dismally small for sharks), Distinctive Characters, Additional Description (generally brief), Color, Size, Developmental Stages, Habits, Relation to Man, Range, Occurrence in Western Atlantic, and the annotated Synonymy; occasionally with such additions as Food, Abundance, Migration.

Each species is represented by an outline figure, with color pattern added only when striking or diagnostic, supplemented by neat and very useful sketches of significant parts, such as, for sharks, the teeth, the denticles and often the nostrils. The outline sketches of the whole fish have the advantages of uniformity and of economy in preparation and publication (hence practicability), but are neither so recognizable nor so attractive as complete drawings or photographs. One drawback is that, generally, each figure pertains to a single species and is separated by pages of text from figures of related forms. The large page size would allow many species, or diagnostic parts thereof, to be illustrated in a readily comparable way on a single page. Many figures in this volume could have been reduced in size with little or no loss, or even to some gain, particularly if such reduction would bring on one page figures that need direct comparison.

It is clear that a standard of meticulous accuracy has been maintained throughout the vast treatment. Surprisingly few errors of any kind, or inconsistencies, or definitely and obviously wrong judgments, have been seen on first perusal. Some points that seem in need of correction may be mentioned. I think it was a mistake not to report the pelagic lancelet "*Amphioxides valdiviae*" of the western Atlantic as a synonym (postlarva) of *Asymmetron lucayanum*. The lamprey genera *Entosphenus* and *Lampetra* are unsatisfactorily distinguished, in perpetuation of an erroneous observation by Leo S. Berg. It is not true that the ammocetes of *Petromyzon marinus* and species of *Lampetra* are indistinguishable. The family name given (p. 109) as Isuridae should I think stand as Lamnidae. *Tetraoras* (for *Tetroras*) and *angiona* (for *angiova*) (p. 146) are examples of almost non-existent typographical misspellings. The short-snout Atlantic *Scoliodon* (*S. lalandii*) is united with the long-snouted *S. tetracottae* because of "unbroken gradation," but the stated ranges in proportional measurements (p. 299) suggest a rather wide discontinuity and would appear to argue against the suggestion of past interspecific hybridization. *Carcharhinus floridanus* is accorded different authorship on pages 323 and 333. On page 463 *Squalus acanthias* (including *S. suckleyi*, perhaps unwisely) is said to range to the Hawaiian Islands, perpetuating a zoo-geographical absurdity, but on page 473 the Hawaiian records are referred, properly, to another, more tropical species group. It is said on page 478 that *Squalus fernandinus*, of that more tropical type, seems not to range north of southern Argentina, but "the only positive record for Atlantic Argentine waters," as given on page 479, lies off Uruguay. Pigment spots on the back and sides of *Etmopterus hillebrandi* were interpreted (p. 492) as probably luminous, but in this shark as in related species, the vast majority of the photophores are confined to the large blackish ventral areas, in agreement with the general rule that nearly all luminescence in fishes is directed downward.

A few words may be said of the systematic point of view and emphasis indicated in this volume. It is outstandingly masterful as a critical compilation, though it is evident throughout that much of the material available along the Atlantic Coast was examined anew. From the statistical standpoint the treatise can't be rated as strong, even for the few species of which material approaching adequacy was available in museums or on fish docks (it is unfortunate that most sharks are so inconveniently large). There is little evidence of extended studies of variation—geographical, individual or developmental. The stated measurements, for example, are usually restricted to a few dimensions of only one adult specimen or of only one adult of each sex. It is obvious, however, that some generalizations were based on series of measurements that are not detailed (perhaps because they were thought inappropriate in this volume). The nomenclatorial treatment adheres to the International Rules and is otherwise modern. The



systematic judgment is rather conservative, particularly in the frequent assumption of specific identity of long-separated populations that have not been thoroughly compared. However, the decisions are not stated dogmatically and many problems are left open. I strongly suspect that many sharks now treated as cosmopolitan, antitropical types in particular, will prove on detailed comparison to be divisible into several local species or subspecies.

In several ways this volume has been successfully adapted, in line with the policy set for the series, for the use and interest of sportsmen and general naturalists as well as ichthyologists. Features that lead to this desirable end, but do not seriously impair its usefulness to ichthyologists, include the excellent summaries of natural history information, the limited treatment of internal and particularly of microscopical anatomy, the simplified keys, the complete coverage of the species in the clear-cut illustrations. The long synonymies of species and other systematic minutiae will dumbfound many users and will decrease the popular appeal, but will be outstandingly appreciated by researchers. There has been no forced popularization: the volume is a straight-forward, matter-of-fact, unfrilled presentation of a vast amount of well-organized information.

In these days of high costs, slashed budgets and compromised quality it is especially gratifying to know that this large quarto volume has been printed in an edition of 2,500 (with plates saved for another run if needed), on a special 50 per cent rag paper, with excellent design, composition, typography and binding. The general appearance is indeed handsome. Some would have preferred a more standard and more convenient page size, especially when it is noted that the printed matter covers only 46 per cent of each  $9 \times 12$  inch page (a page 0.7 as large would have served adequately). However, one should perhaps not criticize elegance, especially when the price has been held to such a reasonable figure. The authors, the editor-in-chief (John Tee-Van) and his staff (particularly Yngve H. Olsen), the Sears Foundation, and the designers and printers are to be jointly congratulated for bringing to fruition this most auspicious initial installment of a magnificent and much-needed monograph.

We shall all hope for the early appearance of the second volume, to be devoted chiefly to the rays (completing the treatment of the elasmobranch fishes by Bigelow and Schroeder) and to the isospondylous teleosts (by Samuel F. Hildebrand). We understand that the material has largely been completed and trust that the recent, lamented death of Sam Hildebrand will not induce any undue delay.—CARL L. HUBBS, *Scripps Institution of Oceanography (University of California), La Jolla, California.*

#### HANDBOOK OF FROGS AND TOADS OF THE UNITED STATES AND CANADA.

By Albert Hazen Wright and Anna Allen Wright. Comstock Publishing Co., Ithaca, N.Y.: i-xii + 640 pp., 124 pls., 37 maps. \$6.50.—This is not a review but an appreciation. Once more the herpetological world is indebted to that delightful team, Albert and Anna Wright. The third edition of the *Handbook of Frogs and Toads*, which came out in February, has been thoroughly revised, greatly expanded, and brought up to date. It is a useful tool that should be in every herpetological library. It is not a field manual, but a compilation of the vast store of information gathered by the Wrights in their many years of enthusiastic pursuit and study of American frogs and toads. No one else knows these animals so intimately. We are fortunate to have their lore shared with us.

The Wrights state that: "In a book of this sort evidence ought to be presented without too much youthful certainty or elderly obstinacy." Of the 99 species treated fully, they feel that 29 should have more complete life history available before we can be sure of their status, and cite as an example *Rana hecksheri*, recognized first by its distinctive tadpole and peculiar voice. The queries raised in their discussion of these and other species will be a stimulating challenge to field naturalists to find the answers.

The organization of the book is about the same as in the familiar two earlier editions. There are keys to secondary sexual characters, eggs, tadpoles and adults. Mrs. Wright's beautiful photographs are well reproduced and with the maps give an excellent idea of the live animals and where they live. Above all, it is entertaining reading: try it some night with an accompaniment of Allen's splendid frog voice records.—HELEN T. GAIGE, *Ann Arbor, Michigan.*

## EDITORIAL NOTES AND NEWS

### News Notes

**D**R. ROBERT MERTENS, Director of the Senckenbergisches Museum in Frankfort, a M., is in the United States as a member of the University of Chicago—University of Frankfort exchange. He has made the Chicago Natural History Museum his base, and will attend the annual meeting of the A.S.I.H., of which he is an Honorary Foreign Member.

KARL P. SCHMIDT, as delegate of the Society, attended the meetings of the American Institute of Biological Sciences and the Section for Biology and Agriculture of the National Research Council in Washington, May 4 and 5.

Extra copies of the beautiful colored plate of the races of *Natrix erythrogaster*, published in the last issue of Copeia, can be obtained from the Secretary, EDWARD C. RANEY, Stimson Hall, Cornell University, Ithaca, at a cost of twenty-five cents, postage included.

DR. PAUL H. ESCHMEYER completed his doctorate studies at the University of Michigan and resigned from the Institute for Fisheries Research to accept a position with the State of Missouri Conservation Commission as the technical supervisor of research and management of impoundment fisheries, effective April, 1949.

MR. ROBERT F. INGER has been appointed Assistant Curator of Fishes, Chicago Natural History Museum, effective January 1, 1949. Mr. Inger was formerly Assistant in the Division of Herpetology.

MR. ROBERT H. KANAZAWA has been made Assistant in the Division of Fishes, Chicago Natural History Museum.

WILLIAM L. REAVLEY is now serving as Biologist for the Department of Fish and Game of the State of Montana, at Helena.

DR. ERNEST A. LACHNER, formerly Associate Professor of Fisheries Biology, Pennsylvania State College, was appointed Associate Curator of Fishes, United States National Museum, on May 23, 1949.

DR. NELSON MARSHALL, Director of the Virginia Fisheries Laboratory, has been appointed Dean of the College of William and Mary. Since the College and the Laboratory are formally associated organizations he will continue to serve in the development of this research institution.

### Research on Poisonous Fishes

**D**R. BRUCE W. HALSTEAD, of the Division of Medical Zoology of the School of Tropical and Preventive Medicine, Loma Linda, California, is engaged in a long-range research project on poisonous and venomous fishes. He would appreciate receiving any authentic information regarding instances of stings from venomous fishes or accounts of poisoning from the eating of the flesh of fishes. The emphasis of the work is being placed upon Pacific fishes, but accounts regarding fishes of any area will be welcomed. According to present plans this work will be carried on in co-operation with the Pacific Oceanic Fishery Investigations of the U.S. Fish and Wildlife Service.

**Worcester  
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THE DEPARTMENT OF HERPETOLOGY of the WORCESTER MUSEUM OF NATURAL HISTORY, under the able direction of Curator LEWIS HALL BABBITT and Associate Curator FREDERICK CHAFFEE, has been carrying on, with the assistance of Mrs. BABBITT, a program of herpetological education, with an enthusiastic response from their public. In November, 1948, this herpetological group organized the WORCESTER COUNTY HERPETOLOGICAL SOCIETY. An active program is being carried out, with field studies to supplement the work of a herpetology class.

**Requests**

FRANCIS J. MITCHELL, Department of Herpetology, South Australian Museum, North Terrace, Adelaide is interested in hearing from American herpetologists wishing to enter upon an exchange of publications. He has available a recent paper on the Australian Agamoid genus, *Tympanocryptis*.

P. MAEDER, Blauensteinerstr. 10, Basle, Switzerland, a member of the Society, wishes to exchange or buy live lizards and snakes from North and Central America.



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